Climate Niches of New Zealand's Extinct and Extant Plant Genera

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ABSTRACT

Throughout Earth's history changes in environmental conditions have caused plant species to either adapt or become extinct, however, the drivers of past plant extinctions are poorly understood. This project investigates Cenozoic (66 MYA–present) plant extinctions in New Zealand to understand the impact of climate change on the fate of plants. The climate niches of extant and locally extinct New Zealand plant genera in Australia and New Zealand are analysed to determine the role that climate (temperature, precipitation, seasonality) may have played in the disappearance of many genera during Cenozoic climate changes. Species distribution data for extinct and extant genera from nine plant families and gridded climate data for Australia and New Zealand were used to determine the current climate niche of each genus. Current Australian climate contains analogues for both current and past New Zealand climate conditions. Most of the investigated New Zealand extinct genera (69%) occupy significantly different niches in Australia compared to a closely related extant genus that remain in New Zealand. The specific climate features that differentiate extant and extinct genera are not consistent throughout pairs, with precipitation and seasonality variables causing larger differences between genera than mean annual temperature. This suggests that changes in precipitation and seasonality of both temperature and precipitation are more likely to contribute to the extinction of plant species than changes in mean annual temperature. This study found no relationship between extinction age and the level of climate niche overlap between the New Zealand extinct and closely related New Zealand extant genera in Australian climate space. Niche differences were also explored between the Australian and New Zealand distributions of New Zealand extant genera to determine if niche divergence has occurred, which would suggest some level of adaptation to the cool New Zealand climate that developed in the late Cenozoic. All genera currently extant in New Zealand show large differences between their Australian and New Zealand climate niches. For most genera (73%) this difference is not significant, suggesting niche shift but not complete niche divergence. Overall, understanding the differences in the climate niches occupied by extinct and extant plant genera provides insight into potential climate drivers of historic extinctions as well as the level of adaptation to New Zealand climates of those genera that survived.

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Chapter One

1 INTRODUCTION

Climate is a key determinant of the large scale spatial distribution of plant species and ecosystems (McGill, 2010; Pearson and Dawson, 2003; Willis and Whittaker, 2002). Changes in climate drive evolutionary adaptation (Hoffmann and Sgro, 2011; Parmesan, 2006) and have caused recent and geologic plant extinctions (Cahill et al., 2013; McElwain and Punyasena, 2007; Wing, 2004). These processes need to be understood because plants provide essential resources to all systems on earth. Currently, more than 390,000 species of plants inhabit the earth providing a snapshot of the ever changing biodiversity of the planet (Kew, 2016). Of those species, one in five are at risk of human mediated extinction (Kew, 2016). Recent human caused (anthropogenic) climate change and associated extinctions have raised awareness of the need to understand how climate changes will affect potential biodiversity loss in the future (Bellard et al., 2012). Especially because climate change is predicted to further exacerbate the risk of extinction for many taxa (Cahill et al., 2013; Urban, 2015).

The current geographic distribution of a taxon reflects the spatial distribution of environmental conditions to which the taxon is adapted and has access, such as climate and resources. These distributions result in distinct groups of species adapted to similar environmental conditions, known as biomes (Walter and Breckle, 2002). In a single location a multivariate set of environmental conditions collectively determine if a taxon can survive. These conditions are abiotic (not influenced by living organisms) and include water availability, temperature, irradiance, length of day, and soil type. The suite

of environmental conditions that are suitable for a taxon is considered its niche (Hutchinson, 1957).

At a conceptual level, the niche includes all the abiotic factors a species requires to survive, this is known as the fundamental niche (Hutchinson, 1957). The fundamental niche exists in environmental space and, when projected into geographical space, is associated with the full range of environments in which a taxon could survive. However, taxa rarely occupy their entire fundamental niche due to competitive interactions with other species, the presence of predators and the connectivity of suitable habitat. The niche based on the current distribution of a taxon is typically smaller than its fundamental niche and is called the realized niche (Hutchinson, 1957). As climates change through time, taxa can either move to follow their niche in geographic space, adapt to the new climates that exist in the geographic space they currently occupy, or go extinct.

Extinction of a taxon occurs when the taxon populations fail to persist in areas that were previously occupied. This occurs at multiple spatial scales with small scale extinctions occurring when a taxon is no longer found in an isolated geographic area such as a country or continent. This level of extinction is known as local extinction. When a taxon is no longer found anywhere on Earth it is globally extinct. Extant taxa are those species that currently have viable populations and exist in a specific locality. Both local and global extinctions of plants have occurred throughout geological history with historic extinctions of plants linked to rapid changes in the global climate system (Wing, 2004; McElwain and Punyasena, 2007) but the specific mechanisms for these historic extinctions are often unknown.

In addition to historic extinctions, anthropogenic climate change has already caused extinctions (Cahill et al., 2013). The mechanisms for climate change related extinctions vary but include exceedance of biological tolerance levels, mismatched timing of species interactions, increased frequency of disasters, changes in pollinator or disperser abundance, new predators, or changes in competition (Cahill et al., 2013). However,

these mechanisms are mainly based on extinctions of animals and the specific mechanisms of plant extinctions remain poorly understood.

New Zealand and Australia are especially vulnerable to climate related extinctions due to the high number of endemic species and isolated landmasses limiting the extent to which taxa can shift their current range to track suitable climates (Urban 2015). These Australasian regions are less studied than areas with lower extinction risk such as North America and Europe (Urban 2015) and more effort is needed to understand the unique circumstances of extinction risk in this region. Australia and New Zealand are uniquely situated to study climate related extinctions. The two countries have a well-known and shared geologic history including times of similar climate resulting in many shared plant families (Gibbs, 2016). Within these shared plant families, genera that are locally extinct from New Zealand currently exist in Australia. In addition to sharing a geologic and taxonomic history, Australia and New Zealand still contain areas of similar climate enabling comparisons between shared and distinct climate spaces.

Overall, understanding the dynamics of historic climate related biodiversity loss can provide insight into what effect current anthropogenic climate change will have on future biodiversity loss and extinctions (Fordham et al. 2016). This project will explore the mechanisms under which climate has impacted locally extinct and extant New Zealand plant species. This understanding provides further insight into how vulnerable plants are to changes in climatic conditions.

1.1 Research Aim and Objectives

The aim of this project is to understand the patterns of currently occupied climates of New Zealand extant and New Zealand extinct plant genera. This will provide insight into the causes of these extinctions and niche shift events as well as provide understanding of how climate changes may impact species in the future. The main objectives of this study are:

- To understand where past and current New Zealand climates occur in modern Australia;
- To determine how the climates inhabited by locally extinct New Zealand genera differ from closely related extant New Zealand genera;
- To compare the climate niches of currently extant New Zealand genera between their New Zealand and Australia distributions; and
- Finally, to establish which climatic factors contribute the most to differences in occupied climate between extinct and extant genera and between New Zealand and Australian distributions in order to determine whether there is any common climate factor responsible for the extinction of New Zealand genera during the Cenozoic.

Chapter Two

2 THEORETICAL REVIEW

Plant distributions are a factor of multiple mechanisms working over different spatial and temporal scales (McGill, 2010). Climate and geologic history act at large to medium spatial scales to determine where species exist (McGill, 2010). This is seen in cold intolerant plants, such as palm trees living in tropical areas and *Nothofagus* trees being restricted to the Southern Hemisphere due to their Gondwanan history (Swenson et al., 2001; Kissling et al., 2012). As the spatial scale decreases, other factors such as dispersal and species interactions have a greater impact on the distribution of species (Pearson and Dawson, 2003; Willis and Whittaker, 2002; McGill, 2010). The combined effect of climate, geologic history, dispersal, and species interactions determine the extent of a species distribution and can be translated into a species niche. Hutchinson (1957) defines a niche as a multi-dimensional space associated with all the environmental variables in which a species can survive. This fundamental niche may not be realised due to other factors, such as species interaction, acting to restrict a species distribution into its fundamental niche (Hutchinson, 1957). The environmental variables associated with a species' current distribution is considered its realized niche.

Analysis of a species niche can give insight into the drivers of its current distribution and can therefore indicate the importance of the different factors that influence distribution (Maguire et al., 2015). For instance, analysis of the realized niche of a locally extinct species may provide an indicator of which factors (i.e. climate, geologic history, dispersal, or species interactions) influenced its extinction. This is particularly important for plant

species because although plant extinctions have occurred throughout Earth's history, very little is known about the factors influencing these extinctions (Wing, 2004). Australia and New Zealand are uniquely situated to allow this type of analysis. The two continents have a well-known and shared geologic history resulting in many shared plant families (Gibbs, 2016). This section will explore the concept and drivers of species distributions, the niche, plant extinctions, and the biogeography of Australia and New Zealand.

2.1 Drivers of Species Distributions

Where a species is located is the result of a complex set of factors in both space and time. There are currently an estimated 390,000 vascular plant species on Earth which vary in type, number, and abundance of species (known as biodiversity) across different regions (Kew, 2016). On a global scale the biodiversity is highest at low latitudes near the equator, likely due to the positive relationship between energy and water availability and species richness (Gaston, 2000; Kreft and Jetz, 2007; Hawkins et al., 2003).

Although biodiversity is driven by factors such as energy and water availability, the distribution or range of individual taxa is affected by many factors and the importance of each factor differs depending on the spatial scale observed (Figure 2.1). At large spatial scales (global to regional) climate and geologic history are important driving factors of species distributions (McGill, 2010; Pearson and Dawson, 2003; Willis and Whittaker, 2002). Other factors that affect species distributions include dispersal and species interactions. Dispersal acts at moderate spatial scales while species interactions are an important determinant of the areas species can occupy at small spatial scales (McGill, 2010; Pearson and Dawson, 2003; Willis and Whittaker, 2002). This section will look at what effect each factor, climate, geologic history, dispersal, and species interactions, has on the distribution and range of plant taxa. How these factors have influenced the biogeography of Australia and New Zealand is discussed in Section 2.4.

Figure 2.1: Conceptual diagram showing the importance of major factors in determining species distribution or range at different spatial scales. Based on figures and tables in Pearson and Dawson (2003), Willis and Whittaker (2002), and McGill (2010).

2.1.1 Climate

Climate is the average set of weather conditions of a specific location over a specific period of time, usually quantified by factors such as temperature and precipitation, and is a key driver of spatial distribution of species on Earth (McGill, 2010). All plants live within a set of environmental tolerances to which they have adapted (Walter and Breckle, 2002). In general, these species would not survive or be able to sustain viable populations outside of their adapted climates, thus constricting their distribution. The clearest examples of the importance of climate on species distribution is seen in the expansion and contraction of species distributions with historic and recent climate change (Lenoir and Svenning, 2015; Walther et al., 2002).

During the last 21,000 years, climate has undergone cycles of change ranging from cold glacial to warm interglacial periods. Between the Last Glacial Maximum (LGM) and present, many plant range shifts have been documented. In China during the LGM, steppe and desert vegetation covered a broader area and extended further south and east than its present day northern restricted distribution, suggesting that climates were drier in Eastern China during the LGM (Yu et al., 2000). Oak and spruce species in Eastern North America have shown a distinct northward migration since the LGM as a response to warming climate (Prentice et al., 1991; Davis and Shaw, 2001). A similar response is seen to cooling climates. For example, flowering stonecrops (*Rhodiola* spp.) on the Qinghai-Tibetan Plateau moved to lower elevations and latitudes in response to cooling temperatures between the Last Interglacial and the LGM (You et al., 2018). In addition, Yu et al. (2000) found that during the LGM, broadleaf forests were located approximately 1,000 km southward of their current distribution as a result of cooler temperatures.

In New Zealand during the LGM, cooler temperatures restricted forest growth resulting in grassland covering much of the islands, with only small areas of forest remaining in the northern North Island (Newnham et al., 2013). These forest areas acted as refugia during the LGM with evidence that these forests expanded with climate warming to cover 85 percent of New Zealand by the time humans arrived (Newnham et al., 1999).

In addition to projected range shifts under future climate change, species have already shown responses to recent climate changes. In the Canadian Rockies, *Picea engelmannii* and *Abies lasiocarpa* have undergone upslope migration as a result of a 1.5 ^{O}C increase in temperature (Luckman and Kavanagh, 2000). Osland et al. (2017) found that fluctuations in extreme cold temperatures explained range expansion and contraction of mangroves in the Mississippi Delta over the last 100 years. Temperature is not the only climate factor associated with recent climate change. In California, several vascular plant species have shown a stronger response to water deficit than to increases in temperature resulting in a downhill instead of uphill migration (Crimmins et al., 2011). Climate stability also has a strong impact on mangrove forests' persistence though time, with areas located close to the ocean, which lack extreme cold events, serving as hot spots for recolonization (Osland et al., 2017).

Plants also have the ability to modify physiologic traits to respond to changes in environmental conditions, known as plasticity (Bellard et al., 2012). These changes can be on a short or long-time scale and can occur through changes to vegetative structures or by reducing the energy put into certain biological processes such as the production of seeds. An example of plasticity can be seen in cushion plants in New Zealand that showed reductions in seed production and leaf size after two growing seasons in response to 1 to 3^{O}C warming (Cranston et al., 2015). The opposite effect was found in angiosperms in New Zealand over a longer time period, where present day leaves are smaller and more round than those found in the Miocene, likely resulting from selection during late Neogene cooling (Reichgelt et al., 2017). Climate changes can result in evolution of new species and groups as well as the extinction of species and groups if they cannot evolve or move fast enough. Over time this results in the large-scale global distribution of the species seen today.

2.1.2 Geologic History

Understanding the current regional species composition on earth requires consideration of the history, in geologic time, of that species and location. Throughout geologic history continents have moved, climate has changed, and species have evolved, which all contribute to the current distribution of plants on Earth (Willis and McElwain, 2014). The first gymnosperm plants evolved and radiated on the supercontinent Pangea during the Triassic (248 and 206 million years ago [MYA]) with families such as Araucariaceae and Podocarpaceae developing at this time (Willis and McElwain, 2014). Angiosperms evolved approximately 100 million years later with the first fossil record from the early Cretaceous (139 MYA, Willis and McElwain, 2014). Radiation of angiosperms continued throughout the remainder of the Cretaceous leading to global abundance by the beginning of the Cenozoic (66 MYA; Figure 2.2; Willis and McElwain, 2014).

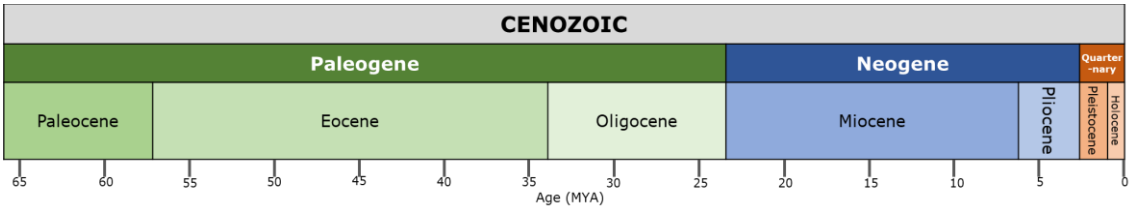


Figure 2.2: Geologic time scale for the Cenozoic period spanning from 66 MYA to present day, based on Walker et al. (2012).

The Cenozoic period is marked by the movement of continental plates into their current position, the formation of major mountain ranges, and development of glaciers at high elevations and latitudes causing global changes to the climate system (Willis and McElwain, 2014). For New Zealand this is particularly important due to the lineages whose history can be traced back to the Southern Hemisphere supercontinent Gondwana (Barker et al., 2007; Swenson et al., 2001; Lee et al., 2012). The beginning of the Cenozoic is marked by warm and wet conditions. Global mountain formation in the Eocene and Oligocene led to the development of arid habitats contributing to the evolution of plants that were adapted to dry and seasonal environments (Figure 2.2, Willis and McElwain, 2014). During the Oligocene and Miocene, steep pole to equator temperature gradients developed as a result of changes in ocean currents due to continental separation (Figure 2.2, Willis and McElwain, 2014). Overall, the Cenozoic shows a marked global cooling trend (Willis and McElwain, 2014) with specific New Zealand trends discussed in Section

2.4.1. In response to these changing environments, species must either move, adapt, or go extinct. This movement, speciation, and extinction of plants throughout the history of earth contributes to the diversity of plants seen today.

2.1.3 Dispersal

Another factor driving the distribution of plant species is dispersal. This ability determines migration distance, contributes to maintaining genetic variability across populations, and may lead to accelerated evolution after separation from the host population (Jordano et al., 2007; Cody and Overton, 1996). The role of long distance dispersal on biodiversity is especially strong on islands (Cowie and Holland, 2006; Kissling et al., 2012). However, other factors also affect biodiversity on islands such as land area and level of isolation (Whittaker et al., 2001).

There are three main mechanisms of plant long distance dispersal: wind patterns, bird migrations, and ocean currents (Gillespie et al., 2012). The directionality of wind events may provide insight into where species originated. For example, many species in the Hawaiian Islands are known to originate in the east which is consistent with the direction of major storms (Gillespie et al., 2012). Other plant species have shown adaptations to facilitate dispersal by birds, such as fleshy fruits or improved germination after passing through a species gut (Fleming and Kress, 2011; Robertson et al., 2006). These adaptations help to facilitate long distance movement of plant species along bird migration routes (Gillespie et al., 2012) and can be seen in the North American source of some plant species on the Hawaiian Islands (Baldwin and Wagner, 2010). Dispersal through oceanic currents is less common than other forms, is typically slow, and requires specialized adaptations for seeds to survive prolonged exposure to salt water (Gillespie et al., 2012). In New Zealand, long distance dispersal, specifically wind and bird dispersal, played an important role in the types of species seen today (McGlone et al., 2001). Those species with long distance dispersal capability have low endemism in New Zealand suggesting recent colonization across oceans (McGlone et al., 2001). Additional information on New Zealand specific dispersal and colonization is found in Section 2.4.2.

Dispersal can act independently but it is also an important mechanism in the face of climate change, facilitating plant movement to areas of suitable climate. Some insects have shown rapid latitudinal and elevation changes in response to current climate changes, moving northward at approximately 1,690 meters/year and moving upslope at approximately 1.1 meters/year (Chen et al., 2011). However, plants are sessile and migration in response to climate occurs at a much slower rate. Dispersal limitation may result in species being unable to reach new climate spaces due to topography, habitat isolation (i.e. alpine areas), or dispersal speed. For example, northward forest migration rates from glacial refugia since the LGM in Europe are approximately 100 meters/year, with tree diversity highest near glacial refugia in southern Europe, even for temperate and boreal species (Svenning and Skov, 2007). Some habitats require large migration rates with approximately 35% of high latitude biomes requiring migration rates of 1,000 meters/year or greater to track their predicted future climate niche (Malcolm et al., 2002). This is of importance because plant migration may not occur fast enough to track future climates. Overall, a species' ability to disperse can determine both where they are located geographically and how well they can respond to changing climates. This is crucial in understanding how species are distributed today.

2.1.4 Species Interactions

Species interactions are also an important driver of species distribution. Species interactions, such as pollination and predation, typically act at small spatial scales (Pearson and Dawson, 2003; McGill, 2010). This can be particularly influential at range margins and may act to restrict a species distribution. For example, reduced pollinator abundance at the edge of a species range has resulted in pollen limitation and eventual reproductive failure, suggesting that pollinators had a larger constraint on range than climate (Chalcoff et al., 2012; Moeller et al., 2012). Herbivory can also restrict plant ranges through direct damage to individuals or seeds (Speed et al., 2010; Freeman et al., 2003). In addition to restricting range, species interactions can also broaden a plant's range. For example, Afkhami et al. (2014) found that the presence of fungal endophytes on the California grass *Bromus laevipes* resulted in improved drought tolerance, resistance to herbivory, and nutrient uptake allowing the grass to expand its range into

drier habitats. Mutualistic relationships may provide long-distance dispersal to some species, such as the New Zealand kea (*Nestor notabilis*) who transport alpine seeds between mountain ranges (Young et al., 2012).

These relationships are important in understanding distributions and can be affected by changes in climate. Many species respond phenologically to seasonal changes in climate, such as flowering and leaf senescence, and climate change has already begun to alter the timing of these events (Walther et al., 2002). Globally, over the last 100 years phenological activity occurred on average 3 days per decade earlier for trees and 5 days per decade earlier for non-tree plants in response to a 0.6^{O}C increase in average global temperature (Root et al., 2003). The timing of flowering in Europe occurs on average 2.5 days per decade earlier, which matches warming trends experienced across Europe (Menzel et al., 2006). Additionally, insect pollinated species show a greater change in timing than wind pollinated species, suggesting a significant link between pollination mechanism and flowering time (Fitter and Fitter, 2002).

These changes in timing of important plant events may result in negative effects for species. For example, the flowering plant *Corydalis ambigua* showed lower seed production during early spring due to a timing mismatch between flowering and pollinator emergence (Gaku and Ida, 2013). Sub-tropical figs at cooler latitudes had reduced reproductive success and lower fitness due to temporal mismatch between pollinators and flowering (Chen et al., 2018). Negative impacts from the mismatched timing between species which depend on a specific interaction for survival can occur on short time scales (e.g. decades), as seen in many species already being impacted due to anthropogenic climate change.

Plants can also have a direct effect on one another through competition. All plants need access to light, water, and nutrients with competition for those nutrients negatively affecting their ability to survive. In Brazil, *Podocarpus lambertii* was shown to have larger growth rates once reaching the upper canopy due to release from competition for light that occurs in the lower canopy (Canetti et al., 2016). In northern Canada, competition between boreal trees was shown to limit tree growth to a greater extent than

climate, demonstrating the importance of direct competition on plant growth (Jiang et al., 2018).

In New Zealand, species interactions have resulted in many specialized plant forms. For example, New Zealand is known for having divaricate shrubs and a plethora of species with small white flowers, both evolved from local species interactions. Divaricate shrubs are characterized by thick intertangled layers of small woody branches covering the outer portion of the plant which likely evolved as a defence against browsing from moa (Bond et al., 2004; McGlone and Clarkson, 1993). The abundance of small white flowers in New Zealand is a result of unspecialized pollination systems, with many species of pollinators visiting the same flower (Newstrom and Robertson, 2005). Species interactions play an important role in determining how species evolve as well as how species are distributed over both short and long time periods.

2.2 Environmental Space and Climate Niches

All geographic areas are associated with a set of environmental variables that are not substantially modified by the presence of living organisms, such as climate, topography, and soils. Combined, these variables make up a multidimensional environmental space as defined by Hutchinson (1957) as a species niche. This type of niche has been termed a Grinnellian niche and is useful at large spatial scales for understanding species distributions (Peterson et al., 2011; Soberón, 2007).

To illustrate, all geographic points in New Zealand are associated with values of annual precipitation and annual mean temperature and these climate variables can be displayed in two dimensions of environmental space (Figure 2.3). This highlights that in New Zealand points that are geographically distant may be climatically similar and vice versa (Figure 2.3). For example, the cities of Christchurch and Greymouth are geographically close (170 km; Figure 2.3a), however, they differ greatly in the amount of annual precipitation they receive and therefore are distant in environmental space (Figure 2.3b). This can be useful for visualizing environmental patterns of large geographic areas (Ackerly et al., 2010).

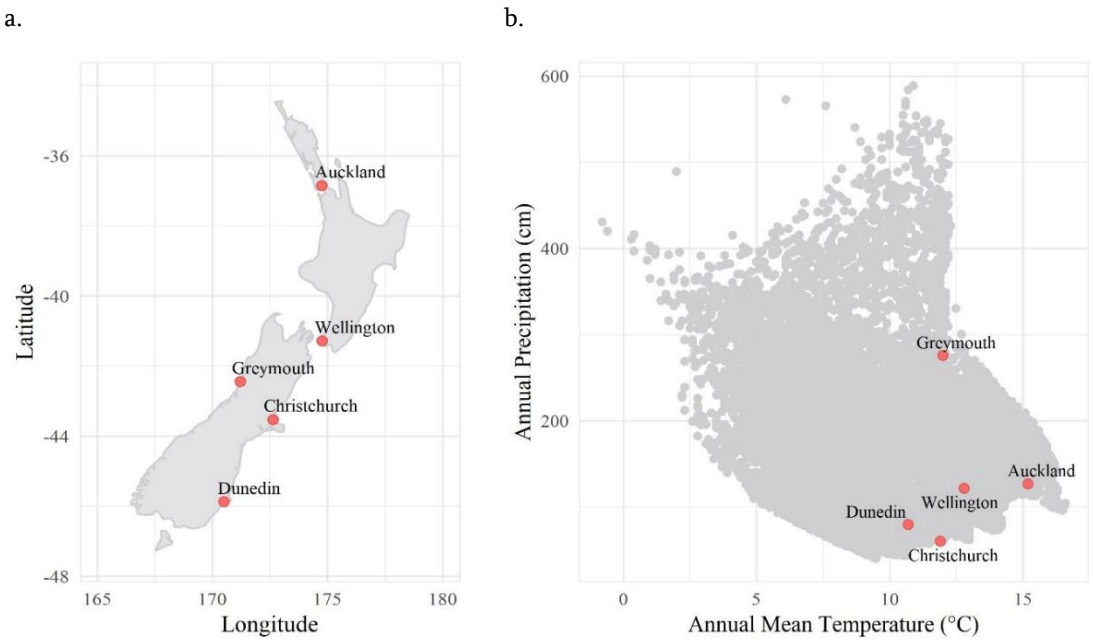


Figure 2.3: The location of New Zealand cities in a) geographic space and b) environmental space. Environmental space is defined in this figure in terms of annual precipitation (y-axis) and annual mean temperature (x-axis).

Variables such as precipitation and temperature can be used to delineate climate space. Observing climate space can show how a particular climate has changed in the past and how it is expected to change in the future. The climate space of an area provides a temporal snapshot of climate conditions that can be compared to the climate space during different times in the past to determine similarities and differences (Garcia et al., 2014). This provides information about the amount and location of analogous climates given predicted future conditions (Fitzpatrick et al., 2018; Veloz et al., 2012; Ohlemüller et al., 2006).

At a species level, the environmental space occupied by a species is considered its niche. On a conceptual level, a niche is the entire environmental space in which a species can survive, the fundamental niche (Hutchinson, 1957). This conceptual fundamental niche is not often achieved by species because other factors influence species' survival, such as competition, which limits the environmental space occupied. The niche associated with a species' current distribution is typically smaller than the fundamental niche and is known as the realized niche (Hutchinson, 1957).

The full realized niche, as defined by Hutchinson (1957), includes all variables not modified by species presence. The climate niche is a subset of a species' realized niche

and specifically refers to the climatic space in which a species occurs. As stated previously, climate is a major driver of species distribution at large spatial scales (McGill, 2010) and therefore the climate niche is an approximation of a species' niche at large spatial scales (Pearson and Dawson, 2003). When scale decreases other variables, such as topography, soil, and species interactions, increasingly influence distribution and should be considered in the analysis of a species realized niche (McGill, 2010; Pearson and Dawson, 2003).

2.2.1 Niches Through Space and Time

Due to the similarity in trait characteristics, closely related taxa (groups of taxonomically related species) generally occupy environmentally and climatically similar areas. This can be seen on a global scale for many species such as scaly tree ferns which tend to occupy areas that are warm, do not experience freezing, and have consistent rainfall (Bystriakova et al., 2011). The palm family (Arecaceae) is also intolerant to freezing conditions and is typically found in areas where the coldest monthly mean temperature is above 5.2 ^{O}C (Reichgelt et al., 2018).

Niches of one or more closely related taxa can either change (niche divergence) or remain the same (niche conservation) over geologic time and space (Figure 2.4, Pearman et al., 2008a; Nogues-Bravo, 2009). Understanding how taxa niches change in space and time help to better interpret findings from niche analysis (Pearman et al., 2008a; Nogues-Bravo, 2009).

Niche Divergence:	The tendency for one or more closely related taxa to change its niche over time or space
Niche Conservation:	The tendency for one or more closely related taxa to have similar niches over time and space

Figure 2.4: Definition of the two types of niche change that occurs over time and space from Pearman et al. (2008a).

Throughout time taxa must move and adapt to different environments, such as global climate change and geographic separation. This can be achieved through migrating in response to climate changes (niche conservation) or adapting to new environmental conditions (niche divergence). Climate niche conservatism since the LGM (21,000 years ago) is seen in several North American plant species despite large changes in climate

during this same time period (Martínez-Meyer and Peterson, 2006). The climate niche of *Laurus* (Lauraceae) in Europe has remained conserved since the middle Pliocene (3 MYA), consistently occupying areas that are warm and wet with little seasonal variation (Rodríguez-Sánchez and Arroyo, 2008). The climate niche of the tree species *Carpinus betulus* and *Picea abies* in Europe have been conserved since the middle Holocene despite large changes in environmental conditions (Pearman et al., 2008b). Other species have responded to environmental changes through niche divergence as seen in European *Juniperus communis* whose niche has diverged from its middle Holocene niche likely due to changes in habitat and competition dynamics rather than climate tolerance (Pearman et al., 2008b).

In addition to climate change over time, niche divergence and conservation may also result from geographic separation deriving from either movement of continental plates or long-distance dispersal. Bystriakova et al. (2011) found that although most scaly tree ferns' niches have been stable through time, some taxa show niche divergence in species that are geographically separated. High inter-genera variance in the climate niches was also partially explained by differences in geographic distribution for *Alsophila* and *Sphaeropteris* (Bystriakova et al., 2011). Dispersal capability also affects the ability of a species to undergo niche divergence. Aguilee et al. (2016) found that species with higher effective pollination distances were more likely to undergo niche divergence due to increased genetic flow and ability to adapt to conditions in newly available climate areas.

A recent and major form of long-distance dispersal is through human mediated invasion of new geographical areas where the invading species may undergo niche divergence due to its release from competition or access and adaptation to new environments not available in their native range. This has been seen in introduced species, such as spotted knotweed, which currently occupies a different niche than its host population (Pearman et al., 2008a). However, this is not always the case. Ebeling et al. (2008) found no niche divergence between the native and invasive range of *Buddleja davidii*, the ornamental butterfly bush, which is native to China and has invaded Europe.

Niche shift over space and time can occur in many ways. Guisan et al. (2014) proposes a unified methodology for observing niche shift through comparing the niche of the old and new (or native and invaded) species range. Specifically, Guisan et al. (2014) proposes three measures of niche shift: stability, expansion, and unfilling (Figure 2.5). Stability, expansion, and unfilling give insight into the type of dynamics occurring within the old and new niches. Niche stability (Figure 2.5d) is a metric that indicates the climate areas used by both the old and new ranges (Guisan et al., 2014). Niche unfilling (Figure 2.5c) refers to those areas that were occupied by the old range and available to the species in the new range but the new range is not using (Guisan et al., 2014). Niche expansion (Figure 2.5e) is the climatic area that is available to but is not occupied by the old range but is occupied by the new range (Guisan et al., 2014).

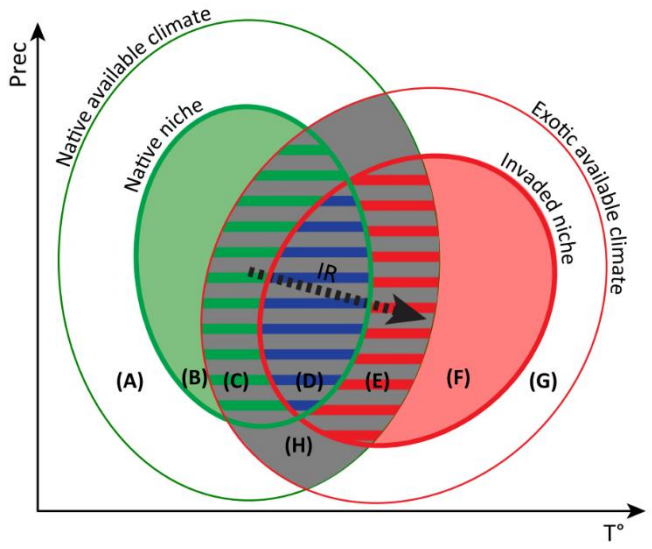


Figure 2.5: Shows the different measures for niche shift between old (native) and new (invaded) species ranges. The measures include a) available climate conditions in the native range, b) native range climate niche, c) unfilling area of the invaded niche, d) stability of the native and invaded niche, e) expansion of the invaded niche, f) invaded range climate niche, and g) available climate conditions in the invaded range. From Guisan et al. (2014).

Spatial scale may affect the level of niche shift occurring. Emery et al. (2012) found high levels of niche divergence between *Lasthenia* species (California grass) at the smaller habitat scale but niche conservatism at the broader climate level scale suggesting that competition and local adaptation may play a large role in determining small scale species niche divergence but not at the large scale. Overall, the degree to which niches are conserved or diverged should be taken into account when using niche analysis for past

distributions because species climate niches may have changed through time and space (Nogues-Bravo, 2009).

2.3 EXTINCTIONS

Biotic species extinctions have occurred throughout Earth's history (Willis and McElwain, 2014; McElwain and Punyasena, 2007; Wing, 2004). For plants, changes in climate can cause extinctions through a range of factors including both abiotic and biotic mechanisms. Abiotic causes of extinction relate to direct changes in climate such as exceeding biological tolerance levels, mismatched timing of species interactions, or increased frequency of disaster events (Cahill et al., 2013). Biotic causes of extinction usually relate to indirect changes in biotic interactions from shifting climate such as changes in pollinator or disperser abundance, new predators, or changes in competition (Cahill et al., 2013). These biotic factors may play a larger role in causing extinctions from climate changes than the impact of abiotic factors alone (Cahill et al., 2013). Urban (2015) found that species with specific mutualistic interactions or limited dispersal ability had an increased risk of extinction by up to 6%.

If plants are unable to adapt to these factors of changing climate, they will no longer be able to survive (Christmas et al., 2016). Extinction patterns are often exhibited regionally with the genera or species occurring elsewhere globally. The scale of local extinction can vary. For example, a species can be locally extinct from a small area, such as a national park, or locally extinct from a larger area, such as a county. If a locally extinct species is not found elsewhere then the species is considered globally extinct. This section will explore the history and drivers of plant extinctions on earth.

2.3.1 Plants and Extinctions

Mass extinction events are characterized as a period in which a large portion of the biota goes extinct. In the history of Earth there are five recorded mass extinction events: the end Ordovician (445 MYA), late Devonian (375 MYA), Permian-Triassic (251 MYA), Triassic-Jurassic (200 MYA), and Cretaceous-Paleogene (66 MYA). The most well know extinction event is the Cretaceous-Paleogene resulting in the extinction of the dinosaurs (Feulner, 2009).

These mass extinction events are primarily linked to the extinction of animal species while plant extinctions are less common. In fact, only three of the five mass extinctions are correlated to extinctions in the plant fossil record: Permian-Triassic, Triassic-Jurassic, and Cretaceous-Paleogene (Wing, 2004). These extinctions were characterized by large changes in stable carbon isotopic composition which indicates disturbance in the global carbon cycle (McElwain and Punyasena, 2007).

Only one of these time periods is considered a mass extinction event in the plant record, the Permian-Triassic; the other two events show only localized extinction impacts (Cascales-Minana and Cleal, 2014; McElwain and Punyasena, 2007). An additional plant mass extinction event occurred at the Carboniferous-Permian (305 MYA) but is not considered a mass extinction in the animal record (Cascales-Minana and Cleal, 2014; Wing, 2004). Therefore, only two mass extinction events have involved plants, suggesting that plants are less susceptible to mass extinction than animals. Wing (2004) suggests three explanations for the differing patterns between plant and animal mass extinctions, resulting from plants being:

- Physically resistant to destruction – including the ability to regrow after harm and having long living resilient seeds.
- Sessile – requiring individuals to be resilient in the face of changing conditions and having the ability for long distance dispersal to seek out new habitats.
- Requiring simple resources – all plants can obtain essential resources from the atmosphere and soil through photosynthesis. This differs from animal communities which rely on other trophic levels.

The Carboniferous-Permian is the first mass extinction in the plant fossil record and up to three plant families every million years became extinct during this time period, including Flemingitaceae, Urnatopteridaceae, Tedeleaceae, and Diaphorodendraceae (Cascales-Minana and Cleal, 2014). This extinction is widely seen in peat deposits in North America and Europe that show between 67 and 87 percent of plant species did not survive this period (Wing, 2004). This was likely caused by the disappearance of wetland

and tropical areas which held a large portion of the biodiversity (Cascales-Minana and Cleal, 2014).

During the Permian-Triassic extinction 90% of all marine species (Feulner, 2009) and approximately 55% of plant families went extinct (Cascales-Minana and Cleal, 2014). This time period is associated with climate warming likely due to increased greenhouse gases from volcanism in the Siberian Traps, however causation for the mass extinction event is debated (Feulner, 2009; McElwain and Punyasena, 2007). During this time, changes in the dominant species abundance also occurred including a major loss of gymnosperm species (McElwain and Punyasena, 2007; Hochuli et al., 2010). After this extinction event, a spike in spore abundance indicates that stress tolerant sporophytic lycopsids rebounded more quickly than gymnosperms and were a major part of the post extinction ecology (McElwain and Punyasena, 2007; Hochuli et al., 2010). Areas of Gondwana that were dominated by broadleaf deciduous glossopterids were replaced by needle leaved conifers and pteridosperms, possibly caused by environmental changes such as acidification or warmer temperatures (McElwain and Punyasena, 2007).

The Triassic-Jurassic extinction event is also correlated with increased greenhouse gases from volcanism (Feulner, 2009), however, the impact on plant communities was less extreme with only one plant family (Peltaspermaceae) known to have gone extinct during this period (McElwain and Punyasena, 2007). Cascales-Minana and Cleal (2014) found that plant losses at this time were within the normal background of plant extinctions. Impacts did differ between locations, with areas in North America and East Greenland showing pronounced local turnover in terrestrial plant species assemblages (McElwain and Punyasena, 2007; Barbacka et al., 2017).

The Cretaceous-Paleogene is best known as the event that eliminated the dinosaurs and was likely caused by a meteor impact and volcanism in the Deccan Traps (Feulner, 2009). This period is also associated with plant extinctions. Major changes in compositions and extinction of dominant species is consistent with widespread ecosystem collapse (McElwain and Punyasena, 2007). Interestingly, during this time the fossil record indicates that no flowering plants went extinct in North America (McElwain and

Punyasena, 2007), though increased abundance of early successional ferns following the Cretaceous-Paleogene boundary suggests widespread disturbance of habitat (Wing, 2004).

These extinction events have all been linked to rapid changes in climate, even though the specific mechanism for extinction is unknown (McElwain and Punyasena, 2007). However, not all times of rapid climate change have resulted in plant mass extinctions. The Paleocene-Eocene boundary, a period of rapid climate warming, shows little evidence for plant extinction in the fossil record (Wing, 2004).

Understanding the patterns of previous extinctions may help prevent future extinctions. McElwain and Punyasena (2007) found common patterns among extinction events: plant communities required a long time to recover after the extinction event (up to millions of years), reproductive specialization of plant taxa increased the risk of extinction, and low abundance of plant taxa before the event did not increase extinction risk. Overall, the large diversity of life histories among plants results in higher resistance to extinctions than animals (Wing, 2004; McElwain and Punyasena, 2007).

2.4 Drivers of Australasian Biogeography

The Southern Hemisphere has a marked difference in plant community composition and structure when compared to ecosystems at similar latitudes in the Northern Hemisphere (Leslie et al., 2012). For example, area-based tree diversity is higher in the Southern Hemisphere than in the Northern Hemisphere and the Southern Hemisphere has a slower decrease in diversity with latitude (Burns, 2007). The character of vegetation also differs between the Northern and Southern Hemispheres at similar latitudes. Evergreen broadleaf trees such as *Nothofagus* and *Eucalyptus* dominate Southern Hemisphere forests while conifer (such as Pinaceae) and deciduous (*Quercus* and *Fagus*) forests dominate at similar northern latitudes (Box, 2002).

Geologic history also drives the distribution of plants on Earth. In the Southern Hemisphere this refers to the legacy of plant species on the Gondwana supercontinent. Gondwana began breaking up in the Jurassic Period, approximately 165 to 150 MYA, South Africa separated in the early Cretaceous, and the areas that are now South America,

Australia, and New Zealand remained connected until the late Cretaceous with complete separation of Australia and New Zealand at approximately 80 MYA (Sanmartin and Ronquist, 2004).

2.4.1 Cenozoic Climate and Geologic Movement

Globally, the Cenozoic (66 MYA to present) is marked as a period of tectonic movement and cooling temperatures resulting in the climate patterns seen today (Willis and McElwain, 2014). However, cooling did not occur consistently throughout this period in the Southern Hemisphere. Australia and New Zealand underwent a myriad of changes including climate warming, climate cooling, changes in latitude, and changes in continental size (Prebble et al., 2017; Cooper and Cooper, 1995). These changes are outlined in this section and are important in understanding the current biogeography of Australia and New Zealand.

Paleocene and Eocene

The Cenozoic period began as one of the warmest intervals in Earth's history with maximum temperatures in this time period occurring at the Paleocene-Eocene boundary approximately 56.3 MYA, known as the Paleocene-Eocene Thermal maximum (Willis and McElwain, 2014). This period ended in the middle Eocene, approximately 50 MYA, when global cooling began and continued through the remainder of the Cenozoic period (Willis and McElwain, 2014).

In the early Eocene, Australia and Antarctica were still connected as one continent (Willis and McElwain, 2014). Prior to the separation of Australia and Antarctica, currents originating in tropical lower latitudes dominated the areas around New Zealand and eastern Australia resulting in warmer temperatures than present (Kennett, 1977). Terrestrial temperatures in Australia during this time were warmer than present with mean annual temperature (MAT) in Western Tasmania estimated at approximately 24 ^{O}C at a latitude of approximately 65 ^{O}S (Carpenter et al., 2012; Greenwood, 1994). New Zealand sea surface temperatures were significantly higher than present day with coastal Canterbury having sea surface temperatures up to 30 ^{O}C at a latitude of approximately 55 ^{O}S (Hollis et al., 2009). In present day, coastal Canterbury has an average sea surface

temperature of approximately 13 ^{O}C at a latitude of 43 ^{O}S (Ministry for Environment, 2015).

Australia began to move away from Antarctica in the early to middle Eocene creating the Australo-Antarctic Gulf (Kennett, 1977; Willis and McElwain, 2014; Exon et al., 2001). Throughout the Eocene the shallow South Tasman Rise blocked most of the flow of water from the Atlantic to the Pacific (Exon et al., 2001). As Australia moved away from Antarctica, New Zealand moved east and north away from Australia. This movement was the result of seafloor spreading creating the Tasman Sea with New Zealand reaching its maximum eastward distance from Australia, approximately 2000 km, by the middle Eocene (Lee et al., 2001). Northward movement also occurred with New Zealand moving from approximately 60 ^{O}S in the Paleocene to 50 ^{O}S by the middle Eocene (Lee et al., 2001).

In addition to changes in continental configuration, global CO_2 levels were decreasing as a result of global mountain building and chemical weathering (Willis and McElwain, 2014). These changes resulted in decreasing temperatures in the Southern Ocean during the Eocene. For example, sea surface temperatures near Antarctica decreased from approximately 19^{O}C to 11^{O}C from the early to late Eocene (Kennett, 1977). In New Zealand, sea surface temperature decreased from tropical (30 ^{O}C to 35 ^{O}C) in the early Eocene to approximately 25^{O}C in the middle Eocene (Hollis et al., 2009; Burgess et al., 2008). It is unlikely that terrestrial temperatures in New Zealand ever reached tropical even at their peak, with an estimated average temperature of 20 ^{O}C to 23 ^{O}C during the Eocene (Mildenhall, 1980; Conran et al., 2016).

Oligocene and Miocene

The Oligocene is marked by further global decreases in temperature (Willis and McElwain, 2014). In the Southern Hemisphere, Australia continued to move northward opening the Tasman gateway, the shallow sea barrier between Australia and Antarctica (Kennett, 1977; DeConto and Pollard, 2003; Lyle et al., 2007). This had varying effects with sea surface temperature on the eastern coast of Australia warming up to 5 ^{O}C due to the new inundation of water from the Australo-Antarctic Gulf (Sijp et al., 2011). Overall,

Southern Ocean sea surface temperatures decreased up to 5 ^{O}C in the early Oligocene (Liu et al., 2009; Sijp et al., 2011).

Throughout the Oligocene the Antarctic Circumpolar Current (ACC) developed through deepening of the Tasman Gateway and opening of the Drake Passage, the body of water between Antarctica and South America, to allow a circumpolar deep-ocean current (Stickley et al., 2004). The ACC was established between the late Oligocene and the early Miocene (25 to 23 MYA; Lyle et al., 2007; Pfuhl and McCave, 2005; Livermore et al., 2007). By the middle Miocene, development of the ACC created a steep temperature gradient from the Antarctic to the tropics which had not been seen before its establishment (Kennett, 1977).

In combination with global cooling, Australia continued to move northward allowing the northern portions of Australia to maintain tropical climates despite global cooling while the southern portion changed to a temperate climate (Willis and McElwain, 2014). Species adapted to low mean annual temperature, such as *Nothofagus*, became increasingly present during the Oligocene with temperature seasonality increasing in southeast Australia during the Miocene (Greenwood, 1994).

New Zealand underwent large changes throughout the Oligocene and Miocene. During the Oligocene, marine transgression submerged much of the New Zealand land area (Lee et al., 2001). It is suspected that as much as 80% of the current land area was inundated, resulting in multiple islands (Figure 2.6) and a land area approximately the size of present day New Caledonia (Lee et al., 2001; Cooper and Cooper, 1995). This reduction in land size was accompanied by decreasing temperatures during the Oligocene (Prebble et al., 2017; Cooper and Cooper, 1995). This is witnessed by the increased prominence of *Nothofagus* in northern New Zealand suggesting a warm-temperate climate, similar to that seen in southern Australia (Cooper and Cooper, 1995).

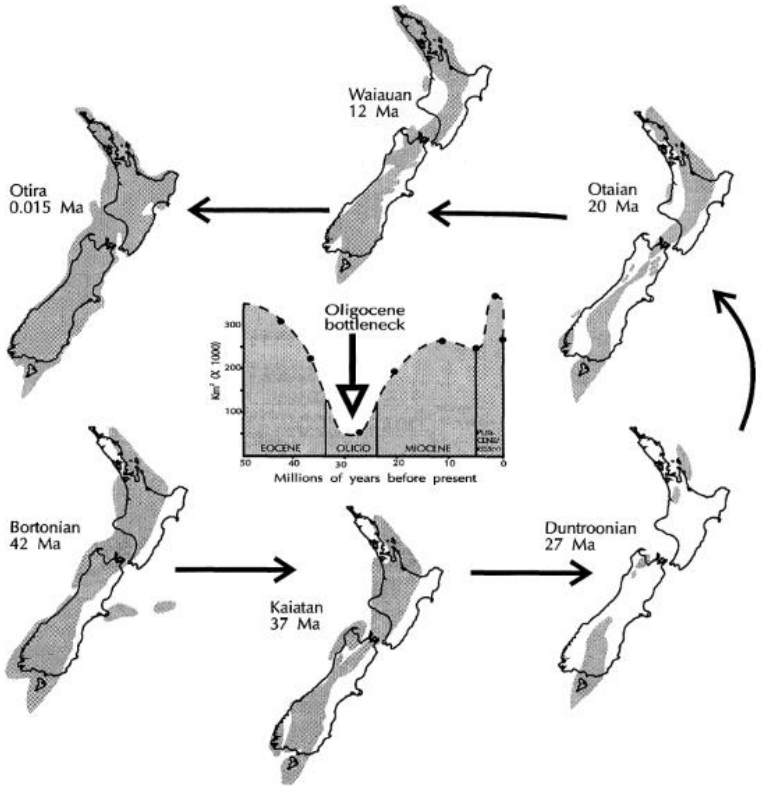


Figure 2.6: Depiction of the total New Zealand land area (grey shading) from the late Eocene to the Holocene. Showing the lowest land area in the Oligocene (shown as Duntroonian 27 MYA). From Cooper and Cooper (1995).

The development of the ACC resulted in varying temperatures surrounding New Zealand with warm water to the west and cool water to the east establishing a humid and temperate climate (Cooper and Cooper, 1995). Average temperatures in New Zealand cooled slightly through the Oligocene remaining relatively stable at around 18 ^{O}C before increasing again in the middle Miocene to between 18 ^{O}C and 20 ^{O}C (Mildenhall, 1980; Devereux, 1968; Pole, 2014; Prebble et al., 2017). Temperature seasonality, calculated as the difference between average summer and winter temperatures, stayed consistent throughout the Oligocene and Miocene at around 6 ^{O}C which is similar to temperature seasonality in present day North Island New Zealand (Prebble et al., 2017). Precipitation remained stable throughout much of this period with mean annual precipitation around 2000 mm, however, precipitation began to increase in the late Miocene in concert with decreases in temperature (Prebble et al., 2017).

By the middle Miocene mountain building began and land area increased to approximately present day size by the late Miocene (Figure 2.6; Lee et al., 2001; Cooper and Cooper, 1995). During this time land was relatively flat compared to today and

susceptible to dispersal from Australia which had similar climatic conditions to New Zealand (McGlone et al., 2001). By the end of the Miocene tectonic activity had begun forming the mountains now present on New Zealand creating cooler climates (McGlone et al., 2001; Greenwood, 1994). The Australian climates at the end of the Miocene were similar to those experienced today (McGlone et al., 2001; Greenwood, 1994).

Pliocene and Pleistocene

From the late Miocene global temperatures continued to cool with a steep drop in temperature at the beginning of the Pleistocene, marking the beginning of the ice age (Zachos et al., 2008; Devereux, 1968; Prebble et al., 2017). Glaciation began in New Zealand approximately 2.5 MYA and continued through the Pleistocene with evidence of at least nine glacial cycles within the last 700,000 years, resulting in much of the South Island being covered in glacial and peri-glacial conditions during a portion of this time (Suggate, 1990). Glaciers were not prominent in Australia with only a few glaciers present in Tasmania and the Snowy Mountains in the southeast (Colhoun and Barrows, 2011; Colhoun, 2004).

The Pliocene and Pleistocene are marked by a sharp decrease in temperature by up to 7^{O}C (Prebble et al., 2017). Temperature seasonality increased during this time to approximately 10 ^{O}C, which is more than is experienced in present day North Island New Zealand but similar to inland and eastern present day South Island New Zealand (Prebble et al., 2017). Increases in precipitation that began in the late Miocene continued through the Pliocene and Pleistocene, reaching an average of 2500 to 3700 mm/year (Prebble et al., 2017).

In the early Pleistocene, the Southern Alps in New Zealand had reached their current height with new alpine areas appearing for the first time in New Zealand (Lee et al., 2001; McGlone et al., 2001). Meanwhile, Australian climates were drying leading to a reduction in forest cover during the Pleistocene (McGlone et al., 2001). This resulted in a marked difference in habitat and climates between Australia and New Zealand (McGlone et al., 2001) which persists to the present day.

2.4.2 Cenozoic Plant Dispersal, Speciation, and Extinction

New Zealand contains approximately 2,500 native vascular species and approximately 82% of those are endemic (McGlone et al., 2001). All of New Zealand's native gymnosperms (20 species) are endemic and there are 1,628 endemic flowering plants (Magnoliopsida; Gordon, 2012). Woody plants have the highest endemism (100 percent) while ferns have the lowest (21 percent), likely the result of differences in dispersal ability (McGlone et al., 2001).

In the millions of years since separation from Gondwana, New Zealand flora has undergone speciation in relative isolation from other landmasses to create new species which are unique to their environments yet have a common Gondwanan ancestry, such as Nothofagaceae, Proteaceae, and many conifers (Barker et al., 2007; Swenson et al., 2001; Lee et al., 2012). Some argue that New Zealand underwent complete submergence during the Oligocene and therefore all of New Zealand's current flora is the result of dispersal after submergence (Trewick et al., 2007). However, there is molecular and fossil evidence that many New Zealand species, such as the endemic *Agathis australis*, occupied New Zealand throughout maximum marine transgression, suggesting terrestrial habitats persisted (Knapp et al., 2007; Lee et al., 2016). Some taxa even display speciation as far back as New Zealand and Australia separation (80 MYA), such as the endemic genus *Fuscospora* (80 MYA; Swenson et al., 2001).

Mountain building following the Oligocene introduced new open and alpine habitats to New Zealand (Heenan and McGlone, 2013). The first colonizers of these areas were likely generalist species favouring open and wet areas including tussock and peat bog environments which became widespread in the Pliocene (Heenan and McGlone, 2013; McGlone et al., 2001). Specialist alpine species evolved in response to the continuous presence of these alpine habitats above the treeline, likely within the last million years (Heenan and McGlone, 2013). Not all Southern Hemisphere plants can trace their origins to the breakup of Gondwana and therefore long-distance dispersal and subsequent evolution may be important drivers of the current plant composition of the Southern Hemisphere (Sanmartin and Ronquist, 2004; McDowall, 2008).

Additions to the New Zealand flora may have been colonized after separation from Gondwana through long-distance dispersal, mainly from Australia (McGlone et al., 2001; Pole, 1994b). Although New Zealand species with spores or barbs, which facilitate dispersal, tend to have higher similarity with Australian counterparts, poor dispersers also share species across the Tasmin Sea (Jordan, 2001). These poor dispersers likely colonized New Zealand when canopies were open and susceptible to invasion potentially after marine transgression in the Oligocene (McGlone et al., 2001). Current endemism in New Zealand appears to be related to the ease with which species can disperse and colonize. This is seen with effective dispersers and colonizers, such as ferns, having low endemism when compared to other species (McGlone et al., 2001).

In addition to vicariance and long distance dispersal, the current New Zealand flora is likely the result of climate cooling (Lee et al., 2001). During the Eocene, Australia and New Zealand were covered by evergreen forests with warm weather species dominant due to warmer temperatures during this time (Utescher and Mosbrugger, 2007). Movement to cooler temperatures in Australia and New Zealand by the Oligocene was seen through an increase in the prominence of the cool adapted *Nothofagus* especially through southern Australia (Cooper and Cooper, 1995). Many flora extinctions also occurred in the late Miocene to Pleistocene due to cooling temperatures (Lee et al., 2016). Specifically, several groups of warm climate trees went locally extinct in New Zealand during this period, including *Eucalyptus* and *Brassospora*, which still occur in either Australia or New Caledonia (Lee et al., 2016).

Many families have a long history in the Southern Hemisphere. Within Araucariaceae, both *Araucaria* and *Agathis* appeared in Australia and New Zealand in the Cretaceous with *Araucaria* going locally extinct in New Zealand in the Miocene (Lee et al., 2016). *Podocarpus* is currently extant in both Australia and New Zealand and also has a long history in the Southern Hemisphere appearing in the South American fossil record in the Cretaceous but not appearing in Australia or New Zealand until the Eocene (Lee et al., 2016). *Microcachrys,* the close relative of *Podocarpus*, has a similar time of arrival with the first appearance in Australia and New Zealand occurring in the Cretaceous (Lee et al., 2016). However, *Microcachrys* went locally extinct in New Zealand in the

Pleistocene (Lee et al., 2016). Overall, changing climate, geologic movement, species dispersal, colonization, speciation, and extinction have impacted the diversity and distribution of species in modern day Australia and New Zealand.

Chapter Three

3 METHODS

To understand climatic patterns of plants that went locally extinct in New Zealand during the Cenozoic, this study quantifies the climate niches of closely related New Zealand extant and extinct plant genera. This will allow us to identify the potential role of different climate factors in plant extinctions. Additionally, understanding how New Zealand extant genera differ climatically from their relatives in Australia will provide information on the amount and type of niche conservation or divergence that has occurred in the years since geographic separation or colonization. Climate niche analysis is used to detect and quantify differences in the realized climate niche between extinct and extant New Zealand genera using current distributions in both New Zealand and Australia (Figure 3.1). This section discusses the data collection and analyses used.

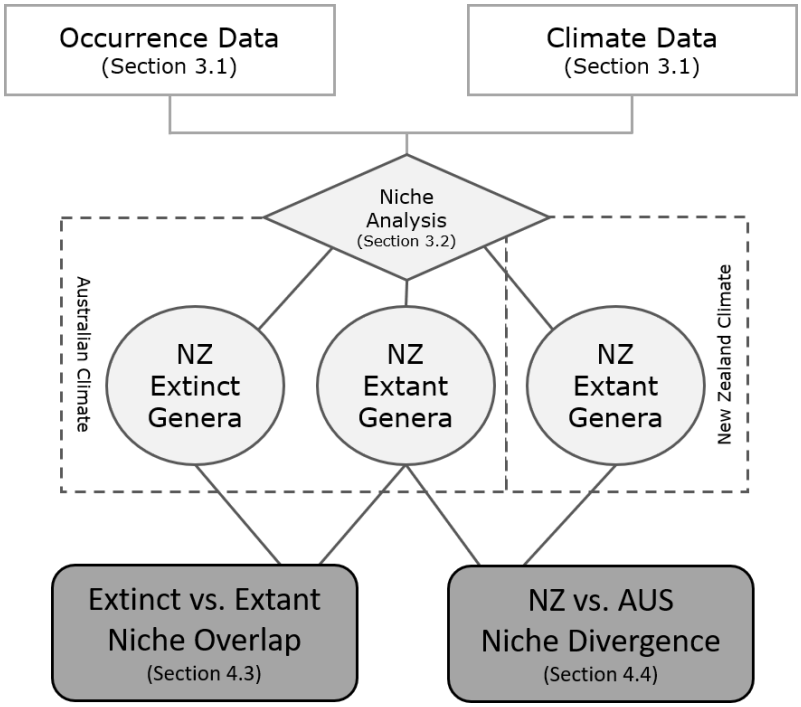


Figure 3.1: Summary of the steps in the climate niche analysis undertaken to determine the role of climate in the local extinction of genera in New Zealand during the Cenozoic.

3.1 Study Area and Data

The first phase of this study included collecting genera occurrence and climate data for the study area. This section outlines the geographical scope investigated, the genera analysed, and the sources of genera occurrence and climate data.

3.1.1 Study Area and Taxa

The project focused on the two main Australasian landmasses, Australia and New Zealand (Figure 3.2). These two landmasses share a Gondwanan biogeographical history and have many distinctive features including high levels of species endemism. New Zealand and Australia (Figure 3.2) have a large number of shared woody plant families and genera due to their common geologic history and historic long distance dispersal between these landmasses (Lee et al., 2001; McGlone et al., 2001; Lee et al., 2016).

Figure 3.2: Location of the Australasian study area landmasses of New Zealand and Australia in the South Pacific

Many New Zealand plant families and genera show widespread Southern Hemisphere distributions. Within these families, some genus-level extinctions have been recorded in the New Zealand fossil record (Table 3.1). For this study, the nine plant families analysed contain genera with long histories in New Zealand of which at least one genus per family is locally extinct in New Zealand, and one genus is currently extant in New Zealand. The extinct genera have a known time of extinction from New Zealand based on the fossil record and currently have native distributions in Australia. The extant genera have native distributions both in New Zealand and Australia. Of the nine plant families investigated here, two are gymnosperms (Araucariaceae and Podocarpaceae) and the remainder are angiosperms.

Table 3.1: Families and genera included in the study. All families have occurred in New Zealand and currently have at least one New Zealand locally extinct and one New Zealand extant genus.

Family	Genera Extinct in New Zealand	Genera Extant in New Zealand
Araucariaceae	*Araucaria*	*Agathis*
Argophyllaceae	*Argophyllum*	*Corokia*
Elaeocarpaceae	*Sloanea*	*Elaeocarpus* *Aristotelia*
Euphorbiaceae	*Mallotus*	*Euphorbia*
Fabaceae	*Acacia* *Caesalpinia*	*Sophora*
Lauraceae	*Cryptocarya*	*Beilschmiedia* *Litsea*
Onagraceae	*Ludwigia*	*Epilobium*
Podocarpaceae	*Microcachrys*	*Podocarpus*
Sapindaceae	*Cupaniopsis* *Mischocarpus*	*Alectryon*

3.1.2 Plant Occurrence Data

The realized climate niche for each genus was inferred from the current geographic range of the genus. Current distributional ranges were obtained using occurrence records from the Global Biodiversity Information Facility (GBIF) which provides global open access species occurrence data. To maintain a standard format between data uploaded from different sources, GBIF uses the Darwin Core Standard (GBIF.org, 2019a). This is a set of standards for facilitating the sharing of species occurrence data (Wieczorek et al., 2015). A subset of the standardized fields was used for this project (Table 3.2) and are discussed further in Section 3.1.4.

Table 3.2: Description of important fields from the Darwin Core Standard used by GBIF (Wieczorek et al., 2015, GBIF.org, 2019a-b).

Field	Description
Country Code	The country in which the occurrence point is located, typically the standard two letter country code.
Locality	Description of the location of the occurrence point, such as, continent, country, state/province, county, municipality, waterbody, island, or island group.
Decimal Latitude	The geographic latitude of the occurrence point.
Decimal Longitude	The geographic longitude of the occurrence point.
Coordinate Uncertainty in Meters	The horizontal distance (in meters) describing the diameter of the circle which contains the extent of the occurrence point. Empty values indicate unknown or unobtainable uncertainty values.
Coordinate Precision	A decimal value indicating the precision of the latitude and longitude coordinates.
Basis of Record	The specific nature of how the occurrence point was collected using specific terminology, examples include "PreservedSpecimen", "FossilSpecimen", "LivingSpecimen", "HumanObservation", "MachineObservation".
Collection Code	The name or code of the collection from which the data was obtained.

Although GBIF provides open source species distribution data, the data contains several biases and inaccuracies. Specifically, GBIF can have a spatial and taxonomic bias with over or underrepresentation of species and locations depending on the origin of the data points (Meyer et al., 2016). Differences in sampling effort may also result in spatial bias which reduces the quality of species distribution models (Beck et al., 2014). Beck et al. (2014) found that in areas with highly clustered data, subsampling to remove spatial bias may be beneficial if the data set is large enough to accommodate reduced sample size.

In addition to bias, errors may exist within the data due to uncertainty regarding taxonomy, such as improperly recorded names, and geography, which may include inaccurately georeferenced points (Meyer et al., 2016). Maldonado et al. (2015) found that geographic inaccuracy was more prevalent than taxonomic uncertainty. Often geographic inaccuracy arises from occurrence points being assigned to political areas instead of precise locations (Maldonado et al., 2015). Geographic inaccuracy can lead to overestimation of species occurrence and richness in areas outside of species ranges (Maldonado et al., 2015; Garcia-Rosello et al., 2015). Therefore, GBIF data was reviewed and filtered to remove taxonomic and spatial bias (See Section 3.1.4). True absences can help to remove spatial bias in species distribution models (Hirzel et al., 2002). However,

only presence data is available through GBIF and this project did not include species distribution models, thereby limiting the impact of missing absence data.

3.1.3 Climate Data

To determine the climate niche of the study genera, plant distribution data was overlaid with climate data. A global climate grid from WorldClim Version 2 was used which consists of spatially interpolated average climate data taken during 1970 to 2000 from up to 60,000 weather stations worldwide (Fick and Hijmans, 2017). All 19 bioclimatic variables were used at a spatial resolution of 4.5 km^2 (Table 3.3; Fick and Hijmans, 2017).

Table 3.3: Climatic variables obtained from WorldClim2 (Fick and Hijmans, 2017) for the study.

Abbreviation	Definition
bio1	Annual Mean Temperature
bio2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
bio3	Isothermality ((BIO2/BIO7)* 100)
bio4	Temperature Seasonality (standard deviation *100)
bio5	Maximum Temperature of Warmest Month
bio6	Minimum Temperature of Coldest Month
bio7	Temperature Annual Range (BIO5-BIO6)
bio8	Mean Temperature of Wettest Quarter
bio9	Mean Temperature of Driest Quarter
bio10	Mean Temperature of Warmest Quarter
bio10	Mean Temperature of Coldest Quarter
bio12	Annual Precipitation
bio13	Precipitation of Wettest Month
bio14	Precipitation of Driest Month
bio15	Precipitation Seasonality (Coefficient of Variation)
bio16	Precipitation of Wettest Quarter
bio17	Precipitation of Driest Quarter
bio18	Precipitation of Warmest Quarter
bio19	Precipitation of Coldest Quarter

The 19 bioclimatic variables used cover a broad range of factors that may impact a species' ability to survive changing climates and therefore need to be considered. These factors can be split into three main groups: temperature, precipitation, and seasonality. Temperature variables (bio1, bio5, bio6 and bio8-10) indicate the average, minimum, and maximum temperatures experienced throughout the year. Precipitation variables (bio12-14 and bio16-19) indicate the average, minimum, and maximum level of precipitation experienced throughout the year. Both temperature and precipitation provide information on the general characteristics of the climate in a location. In addition to

general characteristics, seasonality variables (bio2-4, bio7, and bio15) provide information about the temporal distribution of temperature and precipitation throughout the year. For example, two locations may have the same average yearly precipitation, but one location may get most of their precipitation through large events during one season while another location may have small precipitation events throughout the year. This affects the types of plants that can survive in those locations.

Interpolated gridded climate data provides complete geographic coverage of all climate variables (Ensor and Robeson, 2008). These datasets are considered useful tools for climate niche analysis (Bedia et al., 2013). However, interpolation error occurs in many areas and the accuracy of global interpolated climactic variables is hard to validate (Bedia et al., 2013). For example, mountainous areas have high interpolation error due to a low density of weather stations and high geographic heterogeneity (Hijmans et al., 2005).

Gridded climate models also have a smoothing effect in areas with high spatial climate variability, such as precipitation in coastal areas, which results in more error than in continental climates (Fick and Hijmans, 2017). For example, Ensor and Robeson (2008) found that gridded climate data removed extreme precipitation events that were seen in the observed data. Overall, gridded climate data provides an appropriate representation of climate at large scales.

3.1.4 Data Preparation

Global occurrence data was downloaded for each plant family from GBIF on April 24, 2019 (GBIF, 29 April 2019 a-i). Only occurrence points that had a spatial coordinate reference point and did not have spatial issues, as determined by GBIF interpolation, were downloaded. Further filtering was completed in R statistical software to include only points that:

- were identified as one of the study genera (Table 3.1),
- were located in Australia or New Zealand,
- were collected via human observations or preserved specimen, and
- had geometric uncertainty of less 2,250 meters (which differs from spatial uncertainty mentioned above).

Only those points identified to the species level were included to remove any points which may have been misidentified at the genera level. Points with greater than 2,250 meters spatial uncertainty (i.e. half the size of the climate grid used) were also removed to reduce the likelihood of misclassification of climate variables. Only occurrence points collected via human observations or preserved specimen were used due to the uncertainty and inappropriateness of the other Basis of Record types. Human observations are points based on observation or plot sampling and preserved specimens are from herbarium samples (GBIF.org, 2019b). Fossil specimen were excluded because this study is only interested in the current realized climate niche of each genus and not where the genus occurred in the past. Inclusion of fossil records would also require inclusion of past climate models which were not included in this study. The other classifications were not appropriate, such as cultivated specimens in managed areas (GBIF.org, 2019b).

After filtering the GBIF data, approximately 530,000 occurrence points remained for all nine plant families (Table 3.4). The number of occurrence points per genus ranged from *Microcachrys* with 112 points to *Acacia* with 359,415 points (Table 3.4).

Table 3.4: Summary of the final data used. This includes the number of GBIF occurrence points after filtering, the number of WorldClim2 grid cells that correspond to the GBIF occurrence points, the total number of species per genus within Australia, the total number of species per genus within New Zealand, and the total number of species within both Australia and New Zealand. Orange rows denote genera which are extant in Australia but locally extinct in New Zealand and blue rows denote genera that are extant in both Australia and New Zealand.

Family	Genera	Occurrence Points	Grid Cells	Species in Australia	Species in New Zealand	Total Species
Araucariaceae	*Araucaria*	1,827	661	7	0	7
	Agathis	1,347	338	4	8	9
Argophyllaceae	*Argophyllum*	635	155	4	0	4
	Corokia	1,141	436	2	4	6
Elaeocarpaceae	*Sloanea*	2,355	764	4	0	4
	Elaeocarpus	29,420	6,391	26	3	28
	Aristotelia	10,416	3,027	3	3	5
Euphorbiaceae	*Mallotus*	4,341	1,534	15	0	15
	Euphorbia	19,949	8,899	90	35	107
Fabaceae	*Acacia*	359,415	43,862	1,054	0	1,054
	Caesalpinia	436	225	13	0	13
	Sophora	2,656	1,073	7	9	13
Lauraceae	*Cryptocarya*	17,693	2,701	53	0	53
	Beilschmiedia	13,588	2,187	11	4	15
	Litsea	5,948	1,993	13	2	15
Onagraceae	*Ludwigia*	5,666	2,351	10	0	10
	Epilobium	16,578	6,860	21	48	53
Podocarpaceae	*Microcachrys*	112	44	1	0	1
	Podocarpus	25,802	4,041	10	15	23
Sapindaceae	*Cupaniopsis*	3,329	1,429	15	0	15
	Mischocarpus	1,372	576	11	0	11
	Alectryon	7,839	4,341	15	2	16

Geographic bias may remain within the GBIF data due to clustering of points near highly populated areas. To reduce the effect of clustering, the data was downscaled to match the resolution of the climate grid data. During the downscaling, less than 1 percent of GBIF occurrence points were excluded due to geographic mismatch between occurrence point location and the climate grid. The occurrence data was then linked spatially to the 19 climate variables, the county in which the grid cell occurs, and the occurrence of each study genus (1 for present and NA for no data).

Upon inspection of the final observation data, some points appeared to still occur in areas outside of the known natural range, such as occurrence points in Alice Springs, Australia for *Araucaria* and *Cryptocarya*. Therefore, points which fell above the 99.5th and below the 0.5th quantile for each of the 19 bioclimatic variables were removed. This resulted in

a 7.5% reduction in occurrence related climate grid cells and effectively removed outlying points. After downscaling and removing outliers, genera were associated with approximately 94,000 grid cells (Table 3.4). Acacia was associated with the most grid cells, 43,862 cells (Table 3.4). Without Acacia, there was an average of 2,382 grid cells associated with each genus. These grid cells were used throughout to define the genera climate niche.

3.2 DATA ANALYSIS

After the data was filtered and prepared, analyses were performed to quantify the similarity in the climate niches of the different genera. This included completing a principle component analysis, niche overlap analysis, and comparison of individual climate variables.

3.2.1 Climate Space and Realized Niche

To determine the difference in climate niches this study compared the currently occupied climate niches of extinct and extant New Zealand genera. Environmental space contains a range of variables that interact to create the characteristics of the habitat at a certain location. These variables can be divided into those that are dependent on species presence, such as resource availability or competition, and variables which are not largely dependent on species presence, such as climate (Peterson et al., 2011). Scale can also impact the effect these variables have on plant species. For example, climate acts on the entire range of a species but can also work on a smaller scale to define a habitat, such as topography affecting the temperature of a small area (Peterson et al., 2011). This study focuses on climate variables at a spatial scale of 4.5 km^2.

Climate space is defined as the range of climate conditions present in a given area (Figure 3.3). Changes in climate over geographic space can be quantified by differences in specific climate variables, such as temperature and precipitation. These variables help to describe the type of environment that can be expected within a geographic range. For example, a temperate forest many cover a vast geographic area but be characterized by relatively small variations in temperature and precipitation.

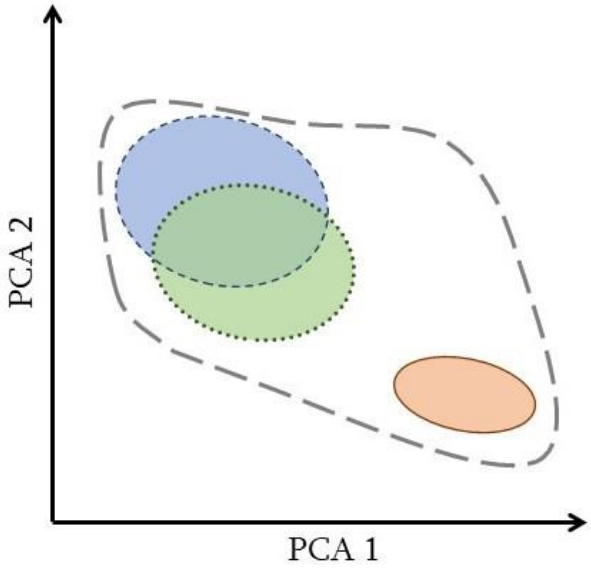


Figure 3.3: Conceptual diagram of the climate space of a landmass (grey dash line) and the realized niche of three genera (blue, green, and orange) in ordination space using two principle component analysis (PCA) axes of climate variables (discussed below).

The concept of climate space has been used to quantify potential ecological changes that may result from changing climates. Ackerly et al. (2010) calculated the climate space of ecoregions in California and Nevada. Through understanding the current climate space, Ackerly et al. (2010) quantified how climate change may alter environmental conditions in geographic space over the next decades.

The climate space of an area was determined by using the WorldClim2 climate grid to obtain climate data for each grid cell in geographic space. To determine the main climate variables across landmasses, a principal component analysis (PCA) was completed on the bioclimatic variables in R (R Core Team, 2019) using the package *ade4* (Dray and Dufour, 2007).

The PCA is a method of ordination which shifts and rotates the coordinate system of a multidimensional point cloud to explain maximum variance (Wildi, 2010). This results in a series or eigenvalues which act as correction values to convert the original values to the PCA axes (Wildi, 2010). New PCA values are used to visualize and analyse multidimensional space in two-dimensions with Axis 1 explaining the most variance and Axis 2 explaining the second most variance (Figure 3.3). Broennimann et al. (2012) found

that a PCA calibrated with the entire study area provided the most accurate measure of climate niche overlap.

To evaluate climate niche difference between extinct and extant genera in a common geographical area the analysis was completed on only the Australian continent (including Tasmania). For this analysis, a PCA was performed on Australian climate space. To evaluate niche conservation and divergence within extant species the analysis was completed for both Australia and New Zealand. For this analysis, a PCA was performed on Australian and New Zealand climate space. To define the realized niche of each study genera, the climate and PCA variables associated with genera occurrence points were extracted.

3.2.2 Quantifying Niche Overlap

After completing the PCA to determine the climate space of the study landmasses and the climate niche of the study genera, the similarity between climate niches was determined. Quantification of these similarities allowed detection of patterns where extinct and extant genera occur in climate space and identified proximate controlling factors.

Schoener's D

To quantify the similarities and differences of the climate niche of paired taxa, the Schoener's D metric was be used (Schoener, 1968). The metric calculates the amount of overlap between niche variables using the equation:

$$D = 1 - {}^{1}/_{2} \sum_{i=1}^{n} \left| P_{x,i} - P_{y,i} \right|$$

Where $P_{x,i}$ and $P_{y,i}$ represents the frequency of occurrence in category i for x and y values respectively. The Schoener's D metric results in a value between 0 and 1 representing no niche overlap to complete niche overlap, respectively (Schoener, 1968). Schoener's D is typically used for niche comparison of microhabitat or diet since $P_{x,i}$ reflects use of these types of biological variables, which may not be appropriate for all environmental niche models (Warren et al., 2008). However, when compared against results from another overlap measure, the Hellinger distance, no significant difference

was observed between the two measures suggesting that Schoener's D is an appropriate measure for environmental variables, such as climate (Warren et al., 2008).

In this study, Schoener's D provides the basis of determining if differences in climate could be the reason certain genera have gone extinct in New Zealand while they are still extant in Australia. For example, when using Schoener's D to compare realised niches of extinct and extant New Zealand genera in Australia, if overlap is low then climate parameters may explain why one went extinct and one remains extant. When used to determine niche divergence or convergence, low Schoener's D indicates the same genus in different ranges occupies different climatic areas and thus underwent niche divergence. Calculation of Schoener's D was completed in R (R Core Team, 2019) using the package *ecospat* (Di Cola et al., 2017). This calculation uses PCA scores to create an occurrence density grid for each genus. Schoener's D is then calculated based on the density grids and corrects for the density of the availability of climates within the study area (Di Cola et al., 2017). Schoener's D is used to compare extinct and extant genera pairs, New Zealand and Australian extant genera distribution pairs, and the niche volume for both sets of pairs.

Niche Similarity

Schoener's D provides a metric of difference but cannot be used to determine if that difference is statistically significant. To determine if niche similarity is significant a niche similarity test was developed by Warren et al. (2008). This test determines if the climate data in the niche of one taxa can predict the niche of another taxa better than expected by chance while incorporating differences in the available climate space between ranges (Warren et al., 2008).

To determine niche similarity, the test calculates niche overlap against a random null model predicting one niche using the other niche. This is calculated over 1000 iterations and the histogram of the null model generated Schoener's D values is compared to the actual Schoener's D value (Figure 3.4). A two-tailed test, similar to the chi-squared test described by Peterson et al. (1999), is completed on the null distribution model to determine if the actual Schoener's D is greater than the 95% confidence interval's upper

value (Figure 3.4, Warren et al., 2008; Broennimann et al., 2012). If the actual Schoener's D is above the 95% confidence interval then the two niches are more similar than expected by chance and niche conservatism is assumed (Warren et al., 2008). This is a widely used metric for determining the level of niche similarity (Dreyer et al., 2019; Hamid et al., 2019; Warren et al., 2008). Calculation of niche similarity was competed in R (R Core Team, 2019) using the package *ecospat* (Di Cola et al., 2017).

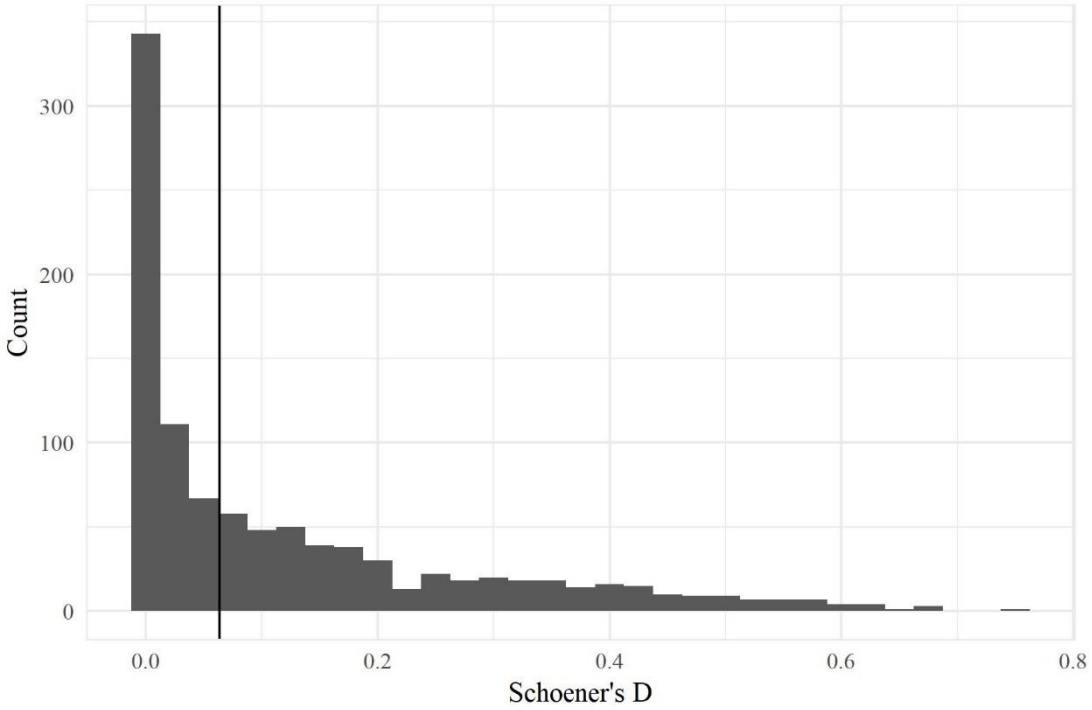


Figure 3.4: Example result from niche similarity test showing the null distribution histogram of 1000 iterations of the random test calculating niche similarity between *Sloanea* and *Aristotelia* in Australian climate space. These niches are not similar due to the actual Schoener's D (vertical line) lying inside the 95% confidence interval (p-value = 0.48).

Raster Analysis

In addition to calculating Schoener's D, niche overlap can be based on a percentage of overlap between different aspects of the niche. Specifically, the amount of niche stability, unfilling, and expansion, as defined by Guisan et al. (2014) was calculated (See Section 2.2.1 for definitions). This is completed by creating one niche grid for each genus distribution as well as for the climate space of each continent. These grids were combined to determine the extent of overlap occurring within similar New Zealand and Australian climate space. This analysis was completed in R (R Core Team, 2019) using the packages *ecospat* (Di Cola et al., 2017) and *raster* (Hijmans and 2019).

Kernel Density

In addition to analysis of overlap in multidimensional climate niche space, each climatic variable was also analysed in one-dimensional space using kernel density. Climatic distributions of genera are not normally distributed and therefore the non-parametric kernel density estimation (KDE) was used. The KDE overlap calculations were competed in R (R Core Team, 2019) using the package *overlapping* (Pastore, 2018).

Kernel density estimation is widely used in niche models. For instance, some species distribution models use KDE to fit a probability distribution to determine where species could occur in environmental and geographic space, especially if niche shape is complex (Blonder, 2018). The KDE are also used in many niche models to create smoothed density of occurrences for determining niche space (Broennimann et al., 2012).This smoothed density of occurrence is the method used for niche modelling in the *ecospat* package (Di Cola et al., 2017).

Chapter Four

4 RESULTS

Comparison of the climate niche of genera can provide insight into which elements of climate are important in controlling distribution. This section provides the results from this investigation. First, the modern Australian climate correlates for past and current New Zealand climates are presented (Section 4.1). Second, an overview of the family and genera geographic distributions, general climate characteristics, and extinction history are described (Section 4.2). Third, to investigate climate signals of past plant extinctions the results of the niche analysis between New Zealand extinct and extant genera are described (Section 4.3). Finally, to determine the level of niche shift between Australia and New Zealand the results of the niche analysis between the Australian and New Zealand distributions of New Zealand extant genera are presented (Section 4.4).

4.1 NEW ZEALAND CLIMATE ANALOGUES

New Zealand climate analogues are those areas associated with current climate, in terms of mean annual temperature and annual precipitation, that are the same as experienced in past time periods in New Zealand. Throughout much of the early to middle Cenozoic, Australia and New Zealand had similar climates with climate differentiation occurring most prominently during the Miocene and Pliocene (see Section 2.4.1). As a result, current climates in Australia and New Zealand are distinct but still share similar characteristics in some areas. Overall, New Zealand is much colder than Australia with average annual temperatures of 10.4 ^{O}C and 21.4 ^{O}C respectively (Figure 4.1a). Winter

minimum temperatures are on average much cooler in New Zealand ranging from - 10.1 ^{O}C to 9.6 ^{O}C while minimum winter temperatures in Australia range from - 5.8 ^{O}C to 22 ^{O}C. Additionally, much of Australia has large differences between winter minimum temperatures and summer maximum temperatures (i.e. large temperature range) with some areas having as much as a 34 ^{O}C difference in central Australia (Figure 4.1c). Coastal areas of Australia have less temperature seasonality and are more similar to the temperature seasonality seen in New Zealand. On average, New Zealand has lower temperature seasonality than Australia with average annual temperature ranges of 19.6 ^{O}C and 27.8 ^{O}C respectively (Figure 4.1c).

New Zealand has higher rainfall on average than Australia with annual precipitation of 1,669mm and 477mm respectively (Figure 4.1b). Specifically, the west coast of New Zealand has substantially higher precipitation than any point in Australia with the highest annual precipitation in New Zealand being 5,886mm and only 3,880mm in Australia (Figure 4.1b). Australia also contains areas with very low annual precipitation, 127mm, while the lowest annual precipitation in New Zealand is higher, 402mm (Figure 4.1b). Precipitation seasonality also varies substantially between Australia and New Zealand (Figure 4.1d). Northern Australia has the highest precipitation seasonality with distinct wet and dry seasons compared with southern Australia and New Zealand (Figure 4.1d). Overall, New Zealand has low precipitation seasonality, with consistent rainfall throughout the year (Figure 4.1d).

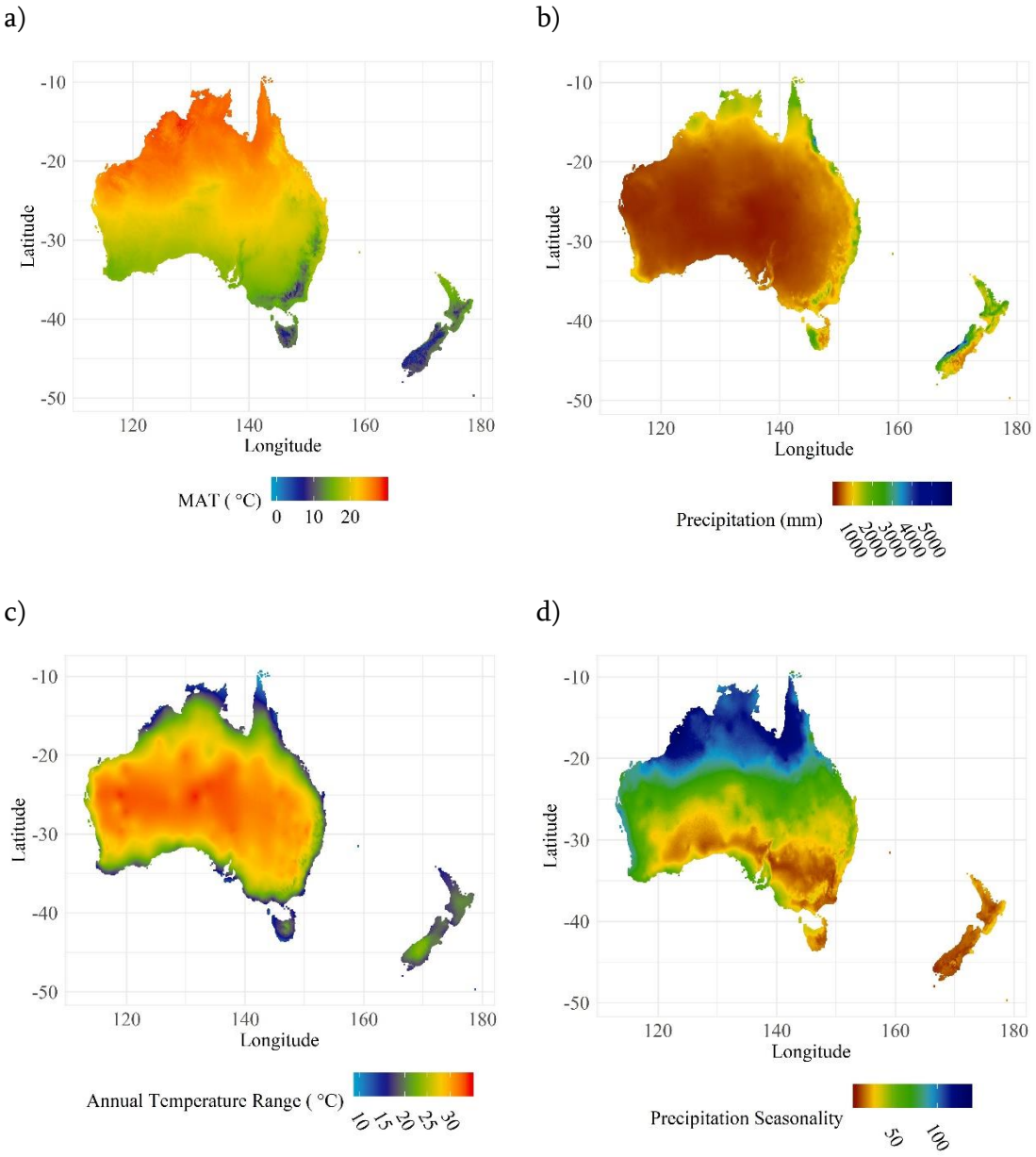


Figure 4.1: Maps showing the a) mean annual temperature (MAT), b) annual precipitation, c) annual temperature range, and d) precipitation seasonality (measured as the coefficient of variation) in Australia and New Zealand from WorldClim2.

4.1.1 Historic New Zealand Climate Analogues

Understanding where analogues for New Zealand's past climates exist in the current climate of Australia can provide an understanding for why certain taxa remain in Australia and not in New Zealand. To determine past New Zealand climates, estimates of mean annual temperature and annual precipitation were obtained from literature (Table 4.1). New Zealand cooled throughout most of the Cenozoic with mean annual temperatures as high as 22 ^{O}C in the Eocene and cooling through the Pleistocene (Table 4.1). Precipitation is considered to have remained stable for much of the Cenozoic

at around 2000mm annually, until the Pliocene where it began to increase, with major increases in the Pleistocene (Table 4.1).

Table 4.1: Past climate estimates of New Zealand for mean annual temperature and annual precipitation from Conran et al. (2016); Mildenhall (1980), Prebble et al. (2017), and Pole (2014).

Cenozoic Period	Temperature	Precipitation
Eocene	20-23 ^{O}C	1200mm to 8000mm
Oligocene to Early Miocene	18-20 ^{O}C	1000mm to 2500mm
Middle Miocene to Pliocene	15-18 ^{O}C	1000mm to 3000mm
Pleistocene	<15 ^{O}C	1600mm to 5000mm

In Australia, the most limiting factor of climate analogues for New Zealand is precipitation. Current Australian climate is drier than past New Zealand climates limiting analogues to the coastal areas of Australia (Figure 4.1 and Figure 4.2). Temperature estimates for later time periods, such as the Eocene, have analogues further north in Australia than more recent time periods, such as the Pleistocene (Figure 4.2). Analogues for all time periods cover less than 1 percent of the current Australian land area. The middle Miocene to Pliocene time period is represented by the largest land area at 0.7 percent while the Eocene, Oligocene to early Miocene, and Pleistocene all have a similar extent with approximately 0.4 percent each. Although these percentages are small, they occupy a large land area due to the large overall size of Australia, totalling approximately the size of New Zealand's South Island.

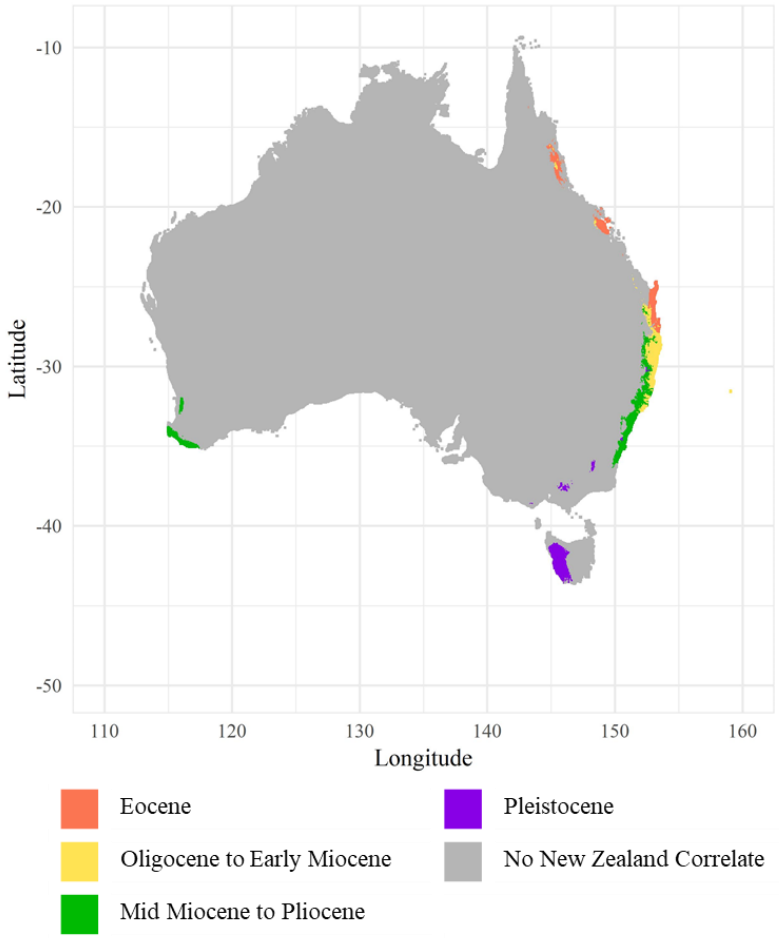


Figure 4.2: Estimated projection of past New Zealand Cenozoic climates in current day Australia based on mean annual temperatures and annual precipitation ranges summarised in Table 4.1.

4.1.2 Current New Zealand Climate Analogues

To understand how a taxon's niche shift has occurred since geographic separation or colonization between Australia and New Zealand it is important to understand where climate analogues for current New Zealand climate exist in Australia and vice versa. Using results of the Australian and New Zealand PCA (see Section 4.4.1), current climate thresholds for New Zealand and Australia were projected onto total climate space. New Zealand climate analogues in Australia occur mostly in the southeast and Tasmania (Figure 4.3). Some areas of similarity extend up the east coast of Australia to approximately 30 ^{O}S (Figure 4.3). In New Zealand, the west coast of the South Island is unique because the region is cool (<10 ^{O}C MAT) and wet (>250 cm precipitation) with no instances of similar climate found in current day Australia (Figure 4.3). Much of the remainder of New Zealand is climatically similar to southeast Australia and Tasmania with moderate annual temperature (between 5 ^{O}C and 20 ^{O}C MAT) and rainfall (between

1000mm and 2500mm precipitation). Overall, 3 percent of Australia's land area contains climates analogous to those of modern day New Zealand and 98 percent of New Zealand land areas has climates found in modern day Australia (Figure 4.3).

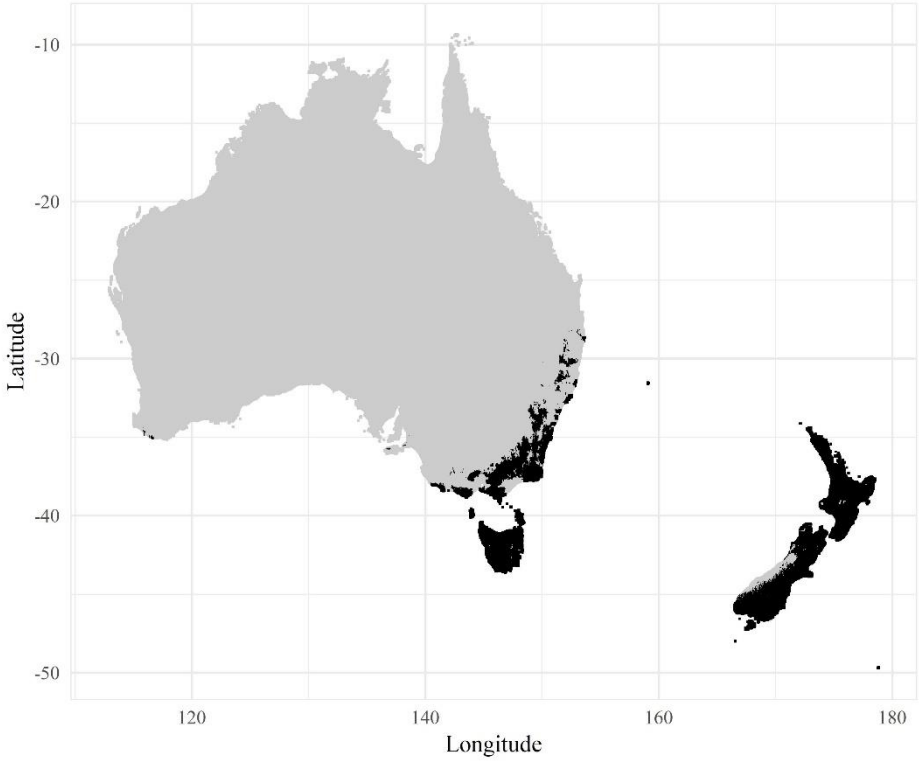


Figure 4.3: Projected climate analogues of current New Zealand and Australian climates. Black regions in Australia have climate that is analogous to New Zealand climate; black regions in New Zealand have a climate that is analogous to Australia.

4.2 Family and Genus Overview

To understand the effect climate has on both extinction and niche shift the general geographic distribution and climate ranges for each family and genus were analysed. This section provides an overview for each family and genus including geographic distribution, general climate factors, and presumed extinction dates.

4.2.1 Geographic Distributions

All nine investigated plant families (Table 3.1) are naturally distributed in both Australia and New Zealand (Simpson, 2010). Four families have distributions restricted to the Southern Hemisphere (Araucariaceae, Argophyllaceae, Elaeocarpaceae, and Podocarpaceae). Two families (Lauraceae and Sapindaceae) are restricted to tropical and temperate regions of both hemispheres. The last three families (Euphorbiaceae, Fabaceae,

and Onagraceae) have more cosmopolitan distributions. Many of these plant families have been cultivated widely for food or ornamentals, resulting in a human mediated distribution outside of their natural range, primarily transported from the Southern to the Northern Hemisphere (Simpson, 2010).

As previously stated, there are approximately 530,000 occurrence points for all nine plant families from the Global Biodiversity Information Facility (see Section 3.1.4 and Table 3.4). The number of occurrence points per genus ranges from *Microcachrys* with 112 points to *Acacia* with 359,415 points (Table 3.4). In Australia, all genera are found on the east coast with many genera found nowhere else in Australia (Figure 4.4). Some genera such as, *Acacia* and *Euphorbia*, are widespread in Australia while others have limited distributions such as *Microcachrys* which only occurs in Tasmania (Figure 4.4). In New Zealand, genera are either widespread, such as *Podocarpus*, or have a northern distribution, such as *Agathis* and *Litsea* (Figure 4.4).

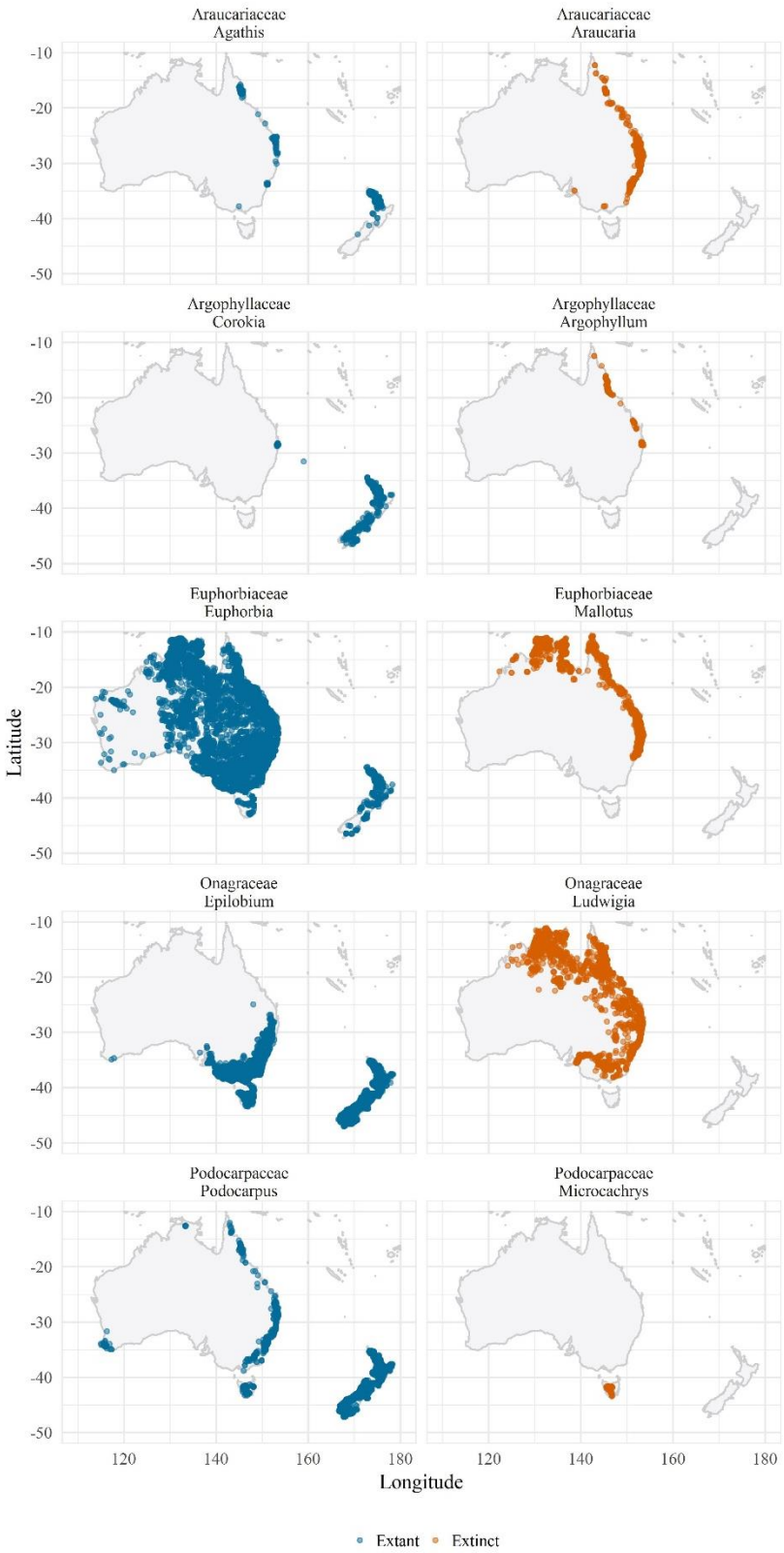


Figure 4.4: Geographic distribution of each genus within the study area. New Zealand extant genera (blue) occupy geographic area in both New Zealand and Australia, while New Zealand extinct genera (orange) currently only occupy geographic area in Australia.

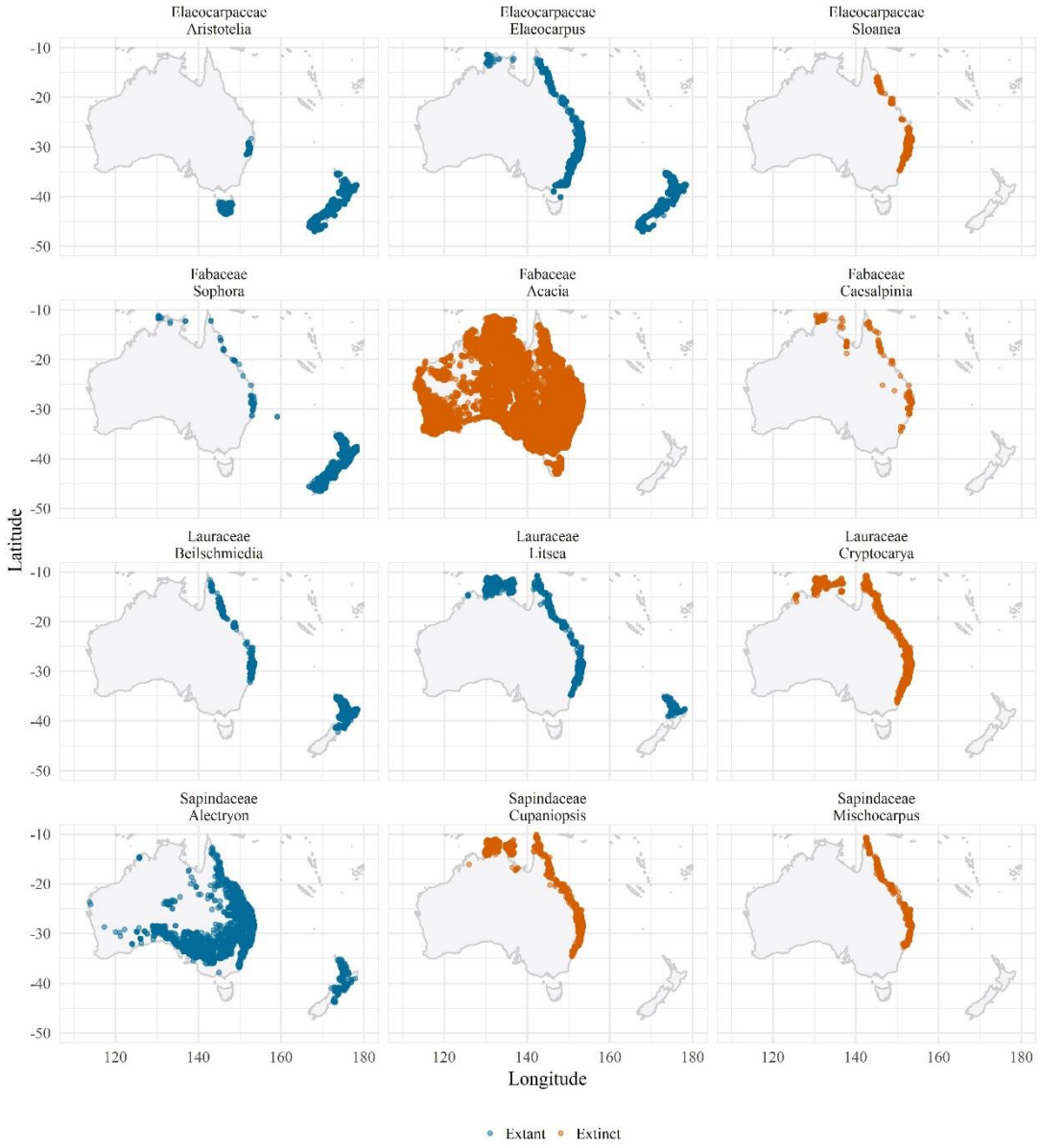


Figure 4.4: continued

4.2.2 General Genera Climate Characteristics

The temperature and rainfall regimes associated with areas that a genus currently inhabits in Australia and New Zealand can give a first indication of differences in climatic preferences of extinct vs extant genera. The study genera occupy a wide range of temperatures varying from average annual temperatures of 2.7 ^{O}C (*Epilobium*) to 28.6 ^{O}C (*Ludwigia*; Figure 4.5) and annual precipitation from 142mm (*Acacia*) to 5,203mm (*Podocarpus;* Figure 4.6). For all families, the range of temperatures occupied by New Zealand extant genera overlaps at least partially with the range of temperatures that New Zealand extinct genera inhabit (Figure 4.5). For most families, New Zealand extant genera generally occur in cooler areas than extinct genera in the same family (except for Lauraceae and Podocarpaceae, Figure 4.5). Overall, New Zealand extant genera have a lower average annual temperature than extinct genera, 14.7 ^{O}C and 19.2 ^{O}C respectively (Figure 4.5). However, the maximum average annual temperature between New Zealand extant and extinct genera are very similar, 28.3 ^{O}C and 28.6 ^{O}C respectively (Figure 4.5).

Unlike temperature, precipitation shows no consistent trend between New Zealand extant and extinct genera within the same family (Figure 4.6). New Zealand extant and extinct genera inhabit areas with similar average precipitation, 1,526mm and 1,419mm respectively (Figure 4.6). However, New Zealand extant genera are found in areas with higher maximum precipitation than extinct genera, 5,203mm and 3,558mm respectively (Figure 4.6).

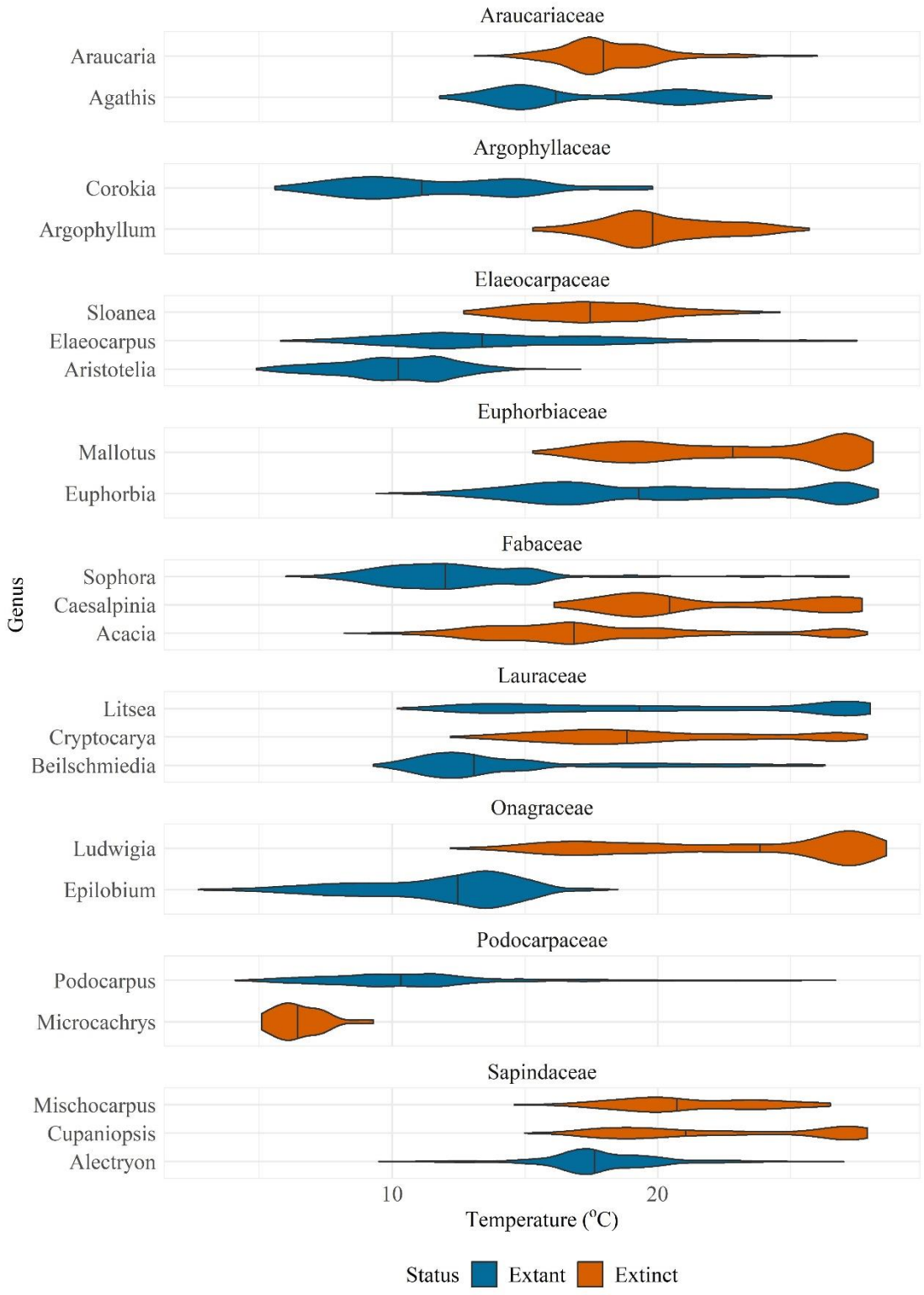


Figure 4.5: Range and distribution of average annual temperature (°C) associated with the geographic distribution of each genus within the study area. New Zealand extant genera (blue) occupy geographic area in both New Zealand and Australia, while New Zealand extinct genera (orange) only occupy geographic area in Australia. Median annual average temperature shown as a black line.

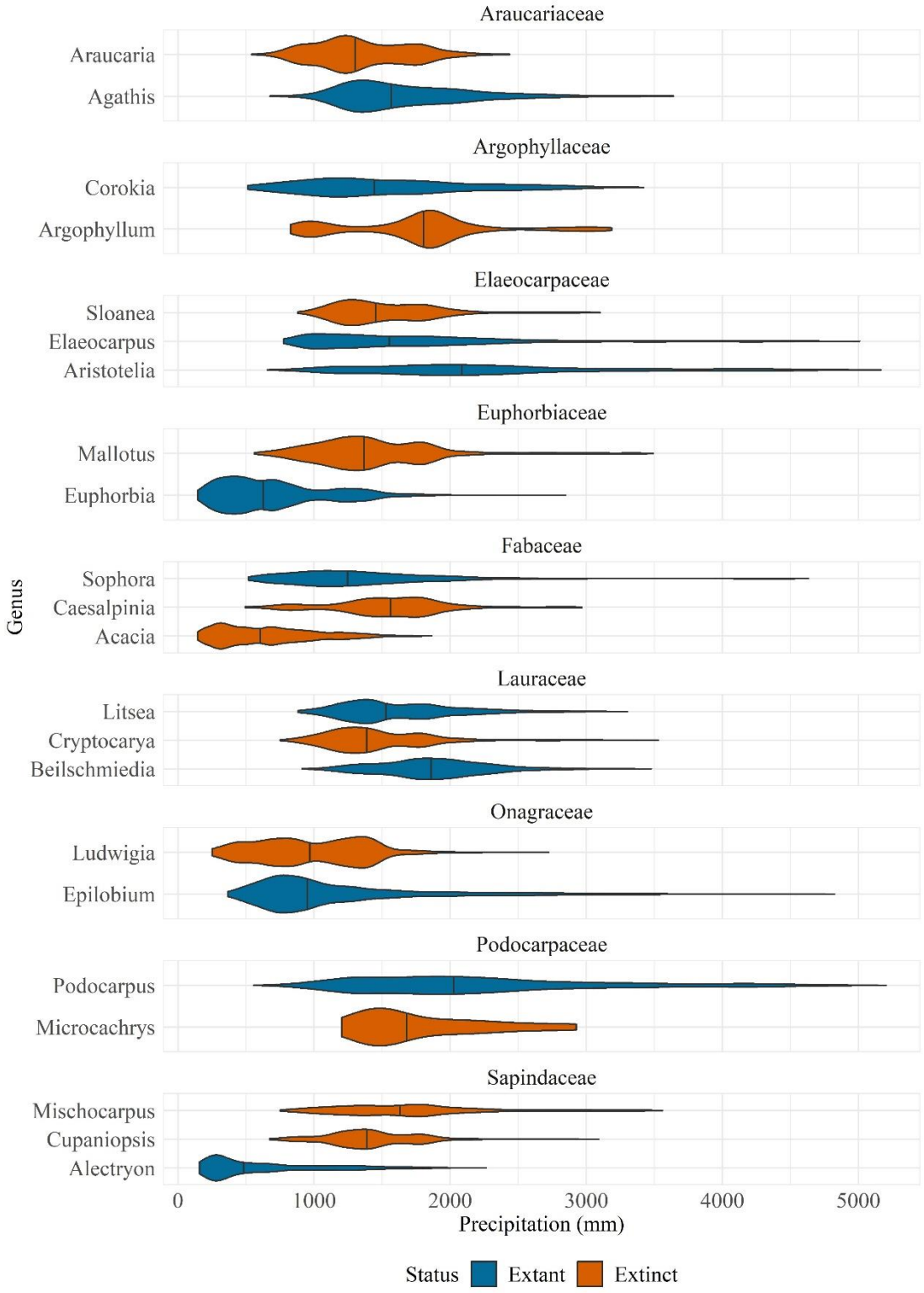


Figure 4.6: Range and distribution of precipitation (mm) associated with the geographic distribution of each genus within the study area. New Zealand extant genera (blue) occupy geographic area in both New Zealand and Australia, while New Zealand extinct genera (orange) only occupy geographic area in Australia. Median annual average precipitation shown as a black line.

4.2.3 Extinction History

To determine the effect of climate on the extinction of each genus it is necessary to know the geologic and climatic history during its presumed date of extinction in New Zealand. The extinction dates are based on the youngest known fossils recorded in New Zealand. The study was designed to ensure half the genera are locally extinct in New Zealand. All the extinctions occurred within the Cenozoic. *Ludwigia* was the earliest extinction, approximately 45 million years ago (MYA), and *Acacia* and *Microcachrys* were the most recent extinctions, occurring approximately 1 MYA in the Pleistocene (Figure 4.7). All other local genera extinctions occurred during the Oligocene and Miocene between 28 and 14 MYA (Figure 4.7).

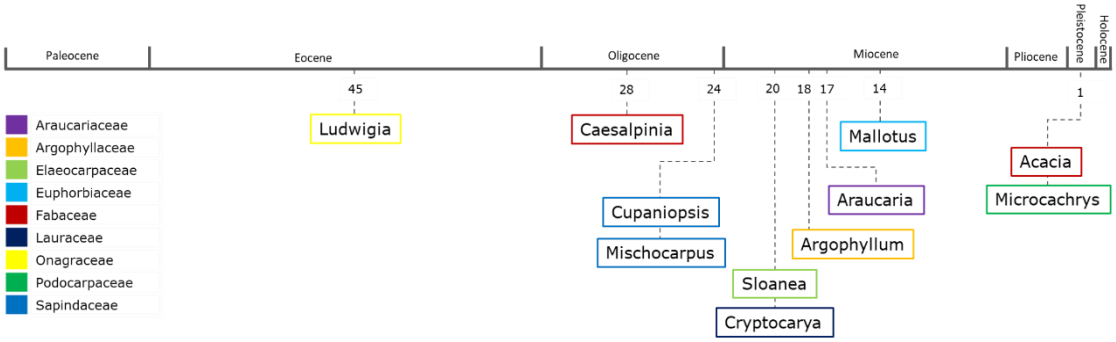


Figure 4.7: Presumed date of extinction from New Zealand for each focal genus. Extinction dates are based on the youngest known fossil record in New Zealand. Dates displayed in millions of years ago (MYA) from Pole (1992); Pole (1995); Pole (2008); Pole (1994a), Lee et al. (2010); Mildenhall (1980); Mildenhall (1989); Raine et al. (2011); Bannister et al. (2012); Pocknall (1989); Jordan et al. (2010), and Conran et al. (2014)

4.3 Climate Niches of New Zealand Extant and Extinct Genera

It is hypothesized that the difference between the climate niche of New Zealand extant and extinct closely related genera (genera pairs) will indicate the climate variables that may have played a role in the extinction of taxa from New Zealand. If extinct and extant genera occupy similar climate niches it is assumed that climate did not play a large role in extinction. If extinct and extant genera occupy different climate niches it is assumed that climate may have played a role in extinction. These assumptions were made because the climate of New Zealand has cooled throughout the Cenozoic while the climate space

available in Australia remained large and relatively stable, albeit drier in central areas, than in the past. Therefore, if extinct genera occupy warmer areas in Australia then this suggests that the cooling of New Zealand climate may have contributed to the extinction of these genera from New Zealand.

The difference in climate niches were determined by observing and analysing the distribution of each genus in climate space. These observations and analyses were completed in Australian climate space because it allows for comparison between niches within common climates and geography. This section provides a description of the principle component analysis (PCA), the relative size of each genus' climate niche, the niche overlap between genera pairs, and the impact of each climate variable on niche difference.

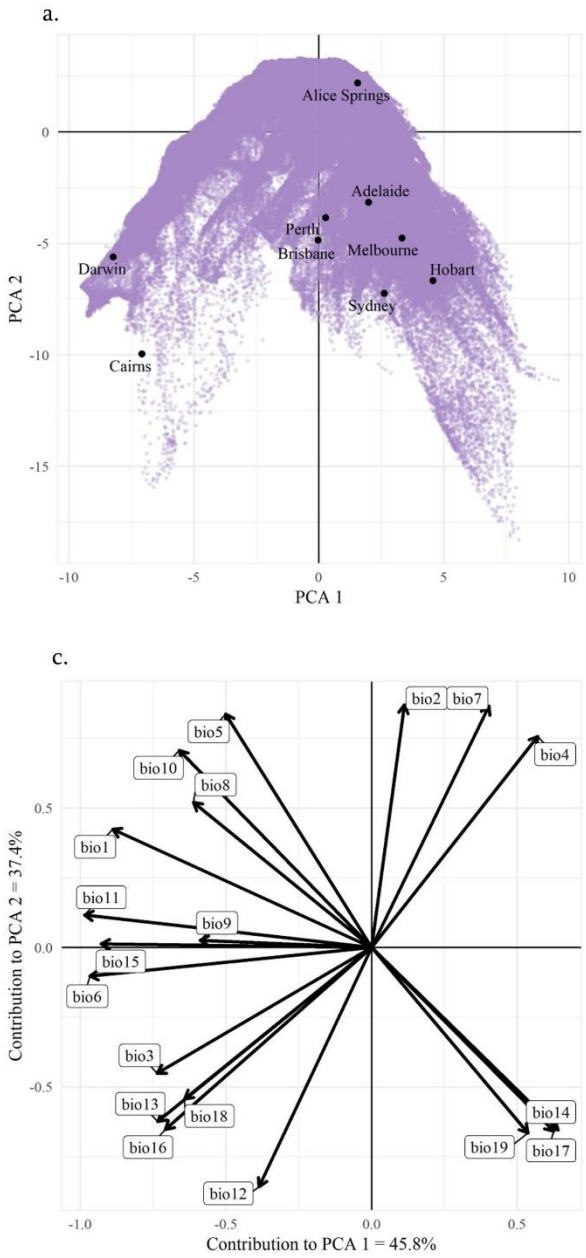
4.3.1 Australian Climate Space

Using all nineteen climatic variables (Table 3.3), a principle component analysis (PCA) was performed on the Australian climate space (Figure 4.8) to extract the two axes that explain the most variation. Australia contains a wide range of climates from sub-tropical warm temperate climates in the Northeast to dry desert climates in the interior. Average annual temperature ranges from 3.9 ^{O}C to 29.5 ^{O}C and annual precipitation ranges from 127mm to 3,880mm (Figure 4.1). The PCA of Australian climate space displays a characteristic horseshoe shape (Figure 4.8a), which indicates a non-linear gradient exists. Specifically, this is the result of plotting two bell-shaped curves, such as those seen in environmental gradients, in two dimensions (Wildi, 2010).

The first axis in the PCA (PCA 1) is highly negatively correlated with temperature and precipitation seasonality variables. Low values along this axis correlate to high annual mean temperature (bio 1), high mean temperature of the coldest quarter (bio 11), high minimum temperature of the coldest month (bio 6), and high precipitation seasonality (bio 15, Figure 4.8c and d). Overall, PCA1 explains 45.8% of the variation in the data. The second axis in the PCA (PCA 2) is highly negatively correlated with annual precipitation and positively correlated with temperature seasonality. Low values along this axis have high annual precipitation (bio 12) and low temperature seasonality,

specifically small diurnal and temperature ranges (bio 2 and 7, Figure 4.8c and d). Overall, PCA2 explains 37.4% of the variation in the data. Cumulatively, the two-dimensional PCA explains 83.2% of the variation in the climate data.

Areas of the Australian climate space with high values along PCA 2 (top portion of Figure 4.8a) are characterized as dry with high temperature seasonality, typified by the town of Alice Springs which is located geographically in the centre of the continent (Figure 4.8a and b). The Australian climate space with low values along both PCA 1 and PCA 2 (lower left portion of Figure 4.8a) reflects warm and wet sub-tropical areas typified by the towns of Darwin and Cairns geographically located in the north and northeast part of the continent (Figure 4.8a and b). The Australian climate space with high values along PCA 1 and low values along PCA 2 (centre to bottom right portion of Figure 4.8a) is characterized as cool with a range of precipitation from drier more temperate areas such as Adelaide and Perth to wetter and colder areas such as Hobart in Tasmania (Figure 4.8a and b).



d.

	PCA 1	PCA 2
Temperature (bio1)	-0.89	0.42
Diurnal Range (bio2)	0.11	0.87
Isothermality (bio3)	-0.74	-0.45
Temp. Seasonality (bio4)	0.57	0.76
Max. Temp. Warm (bio5)	-0.50	0.84
Min. Temp. Cold (bio6)	-0.97	-0.10
Temp. Range (bio7)	0.40	0.87
Temp. Wet (bio8)	-0.61	0.52
Temp. Dry (bio9)	-0.59	0.03
Temp. Warm (bio10)	-0.66	0.71
Temp. Cold (bio11)	-0.99	0.12
Precipitation (bio12)	-0.39	-0.86
Precip. Wet Month (bio13)	-0.73	-0.62
Precip. Dry Month (bio14)	0.64	-0.66
Precip. Seasonality (bio15)	-0.93	0.01
Precip. Wet Quarter (bio16)	-0.71	-0.65
Precip. Dry Quarter (bio17)	0.63	-0.66
Precip. Warm (bio18)	-0.64	-0.54
Precip. Cold (bio19)	0.54	-0.67

Figure 4.8: Results from the principle component analysis (PCA) of Australian climate space used to compare New Zealand extant and extinct genera in Australia. This includes a) the distribution of Australian climate space in two dimensions, b) a conceptual diagram showing the general changes in climatic variables seen in Australian climate space, c and d) the degree and direction to which each climate variable contributes to each PCA axis. PCA axis 1 explains 45.8% of the variance in points and PCA axis 2 explains 37.4% of the variance.

4.3.2 Climate Niche Volume in Australia

Niche volume is calculated for each genus niche in climate space as a metric of the breadth of climates occupied. The size of the genus' climate niche may affect climatic plasticity with genera that inhabit only a small climatic area more vulnerable to extinctions. Therefore, it is expected that New Zealand extinct genera would have a smaller niche volume than New Zealand extant genera in Australia. Niche volume was calculated as the niche overlap (Schoener's D) of a genus' climate niche with the Australian climate space, giving a measure of amount and breadth of climates that are occupied within the available Australian climate space. Niche volume ranges from occupying a low portion of the Australian climate space (*Corokia*) to a moderate portion of the Australian climate space (*Acacia*; Figure 4.9).

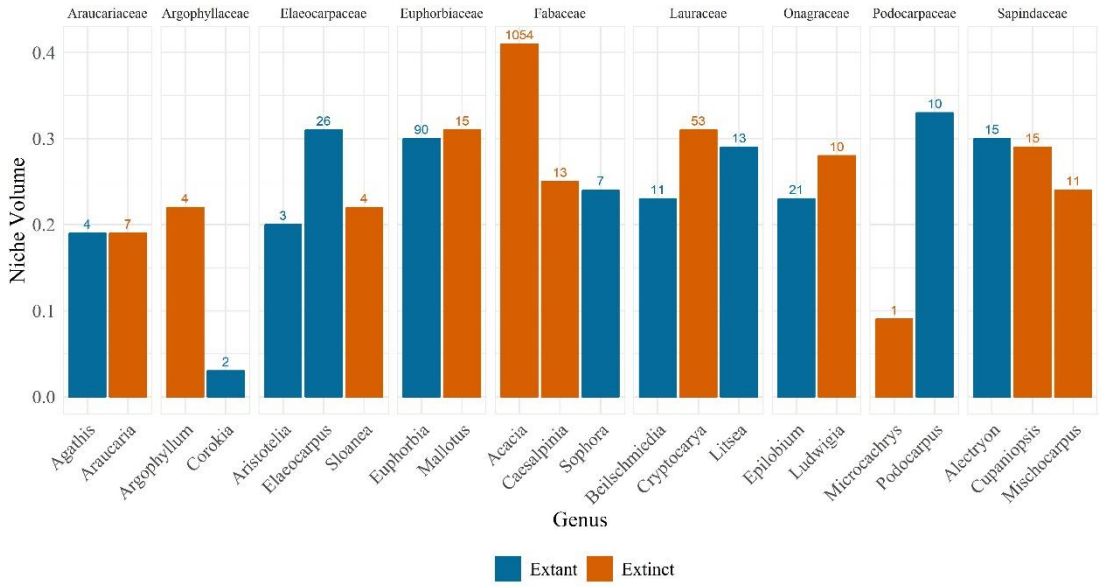


Figure 4.9: Niche volume for each genus in Australia. Niche volume is calculated as the niche overlap (Schoener's D) of each genera niche with the Australian climate space. Numbers on top of bars indicate the number of species within each genus.

Climate niche volume may vary with the number of species within each genus with greater species richness facilitating expanded climate range which may impact extinction risk. For example, within the family Argophyllaceae the extinct genus *Argophyllum* has more species and a larger niche volume than its extant counterpart *Corokia,* four species with 0.22 niche volume and two species with 0.03 niche volume respectively (Figure 4.9). However, this pattern is not consistent across all families, for example within the family Onagraceae the extinct genus *Ludwigia* has fewer species than its extant counterpart

Epilobium but has a larger niche volume, ten species with 0.28 niche volume and 21 species and 0.23 niche volume respectively (Figure 4.9). Overall, there is a positive logarithmic trend between species number and genus climate niche volume (Figure 4.10a) but no correlation is seen between the difference in species number and the difference in niche volume between genera pairs within families (r^2 = 0.006; Figure 4.10b).

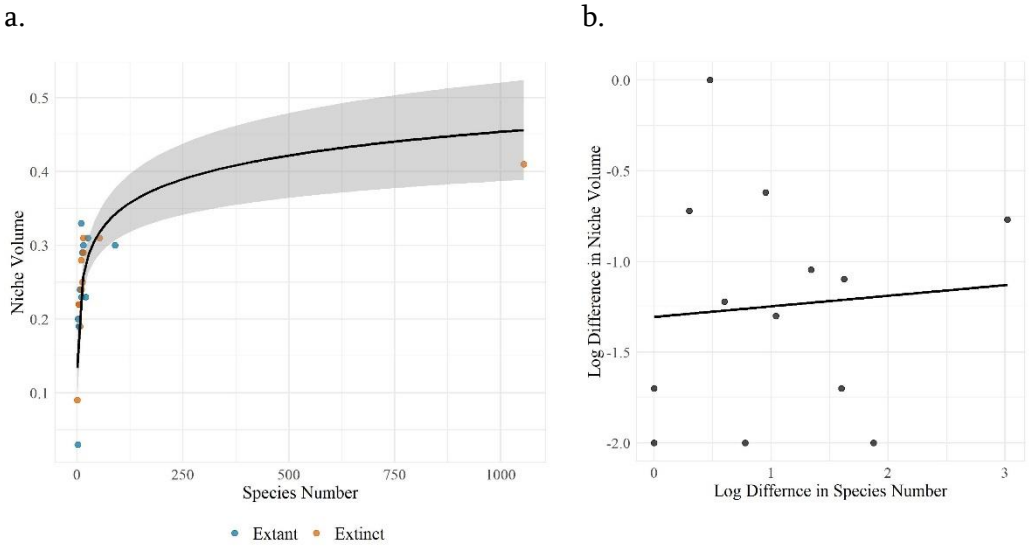


Figure 4.10: Climate niche volume and the number of species per genus in Australia. Niche volume is the amount of Australian climate space occupied by each genus calculated as Schoener's D between the genus niche and Australian climate space. a) Displays the relationship between niche volume and number of species for all genera. b) Shows the relationship between the difference in species number and the difference in niche volume between pairs (r^2 = 0.006).

The Australian climate niches of all genera (both New Zealand extinct and extant) are similar with only a few outlying genera (Figure 4.10 and 4.11). Specifically, *Corokia* (extant) and *Microcachrys* (extinct) both have small climate niches in Australia (outlying points in Figure 4.11) which are also associated with small geographic distributions (Figure 4.4). Overall, no trend is seen between the niche volume of New Zealand extant and extinct genera in Australia with an average niche volume of 0.24 and 0.26 respectively (p-value = 0.68 two-tailed t-test, Figure 4.11). There is no observed link between extinction in New Zealand and current niche volume of extant and extinct genera in Australia.

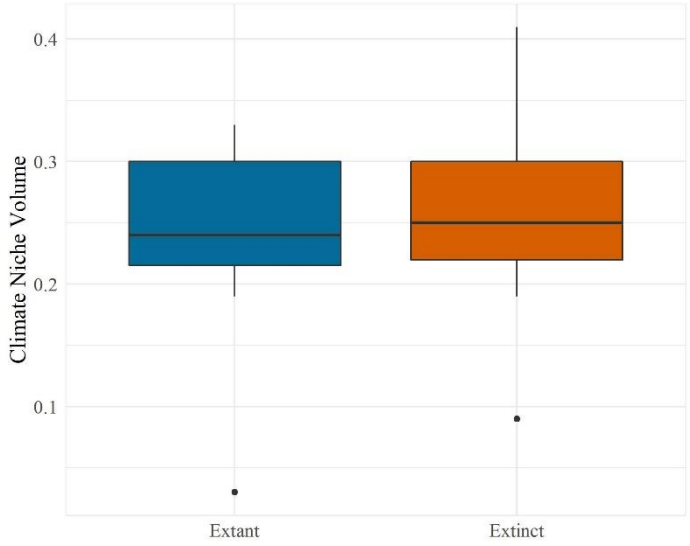


Figure 4.11: No significant difference in climate niche volume between New Zealand extant and extinct genera in Australia (p-value = 0.68, two-tailed t-test). Niche volume is calculated as the niche overlap (Schoener's D) of each genera niche with the Australian climate space.

4.3.3 Extinct and Extant Climate Niches

In order to establish if climate contributed to past extinction events, the current climate niche of closely related genera pairs is compared. If genera pairs of New Zealand extant and extinct genera occupy similar climate niches then it can be assumed that climate was not a factor in the extinction event. However, if the climate niches of genera pairs are different, this suggests that climate may have played a role in extinction. Overall, it is hypothesized that extinct genera will inhabit areas that are different from the climates that currently exist in New Zealand which are on average colder with more precipitation than those in Australia (Figure 4.1).

To determine if closely related New Zealand extant and extinct genera have different climate niches, niche overlap (Schoener's D) was calculated between genera pairs. Schoener's D gives a numeric representation of niche similarity ranging from no overlap (0) to full overlap (1). Genera pairs with low overlap inhabit very different climate niches while genera with large overlap inhabit more similar climate niches. In the focal genera pairs, climate niche overlap ranged from very low, 0.04 (Onagraceae), to quite high, 0.81 (Lauraceae), with an average moderate niche overlap (0.37, Table 4.2).

However, statistical significance cannot be determined based on Schoener's D alone, so the similarity metric was also calculated to determine whether climate niches of genera

pairs are statistically different. Of the thirteen pairs, four pairs were not significantly different (p-value < 0.05, Table 4.2). These pairs were in the families Argophyllaceae (*Argophyllum* vs. *Corokia*), Elaeocarpaceae (*Sloanea* vs. *Elaeocarpus*), and Lauraceae (*Cryptocarya* vs. *Beilschmiedia* and *Cryptocarya* vs. *Litsea*). The remaining nine pairs were statistically different (p-value > 0.05, Table 4.2).

Table 4.2: Results of niche overlap testing for each New Zealand extant and New Zealand extinct pair. Includes Schoener's D metric of niche overlap (0 = no overlap, 1 = full overlap) and similarity test which calculates a significance value for one genus predicting the niche of the other genus (p-value, - = not significant, * = <0.05, ** = <0.01). The similarity test is directional and results are displayed for each direction. Statistically similar pairs are indicated in bold

Family	Pair	Schoener's D	Similarity Test Significance Level	
			Extinct to Extant	Extant to Extinct
Araucariaceae	*Araucaria* vs. *Agathis*	0.23	-	-
Argophyllaceae	*Argophyllum* vs. *Corokia*	**0.21**	*	*
Elaeocarpaceae	*Sloanea* vs. *Elaeocarpus*	**0.78**	*	*
	Sloanea vs. *Aristotelia*	0.06	-	-
Euphorbiaceae	*Mallotus* vs. *Euphorbia*	0.32	-	-
Fabaceae	*Acacia* vs. *Sophora*	0.17	-	-
	Caesalpinia vs. *Sophora*	0.70	-	-
Lauraceae	*Cryptocarya* vs. *Beilschmiedia*	**0.77**	*	*
	Cryptocarya vs. *Litsea*	**0.81**	**	**
Onagraceae	*Ludwigia* vs. *Epilobium*	0.04	-	-
Podocarpaceae	*Microcachrys* vs. *Podocarpus*	0.14	-	-
Sapindaceae	*Cupaniopsis* vs. *Alectryon*	0.31	-	-
	Mischocarpus vs. *Alectryon*	0.25	-	-

In addition to overlap and similarity, the shape and location within the Australian climate space indicates the kind of climatic difference between genera pairs. For three of the four pairs with similar niches, niche overlap is large, and niches are a similar shape (*Sloanea* vs. *Elaeocarpus*, *Cryptocarya* vs. *Beilschmiedia* and *Cryptocarya* vs. *Litsea*, Table 4.2 and Figure 4.12). For the pair *Caesalpinia* vs. *Sophora* there is high niche overlap with a similar shape between genera, however, this pair is statistically different yet with higher overlap than the other statistically different pairs (Figure 4.12).

For the genera pairs with different niches there are three main patterns. The first is where extinct genera inhabit areas that are warmer and often drier than their extant

counterpart. This trend is evident with *Sloanea* vs. *Aristotelia* and *Ludwigia* vs. *Epilobium* (Figure 4.12). The second pattern is where extinct genera occupy wetter, slightly warmer, and more temperate areas than their extant relations. This is seen in the pairs *Mallotus* vs. *Euphorbia*, *Cupaniopsis* vs. *Alectryon*, and *Mischocarpus* vs. *Alectryon* (Figure 4.12). The third pattern is where extinct genera occupy drier areas that are slightly cooler than extant genera which occupy wetter and more temperate climates. This is seen in the pairs *Acacia* vs. *Sophora* and *Araucaria* vs. *Agathis* (Figure 4.12). The final significantly different pair, *Microcachrys* vs. *Podocarpus*, does not show any of these trends with the extant genus occupying warmer climates than the extinct genus (Figure 4.12). The last genera pair (*Argophyllum* vs. *Corokia*) is significantly similar but does not have high niche overlap, likely because the niche of *Corokia* (extant) is completely contained within the niche of *Argophyllum* (extinct, Table 4.2 and Figure 4.12).

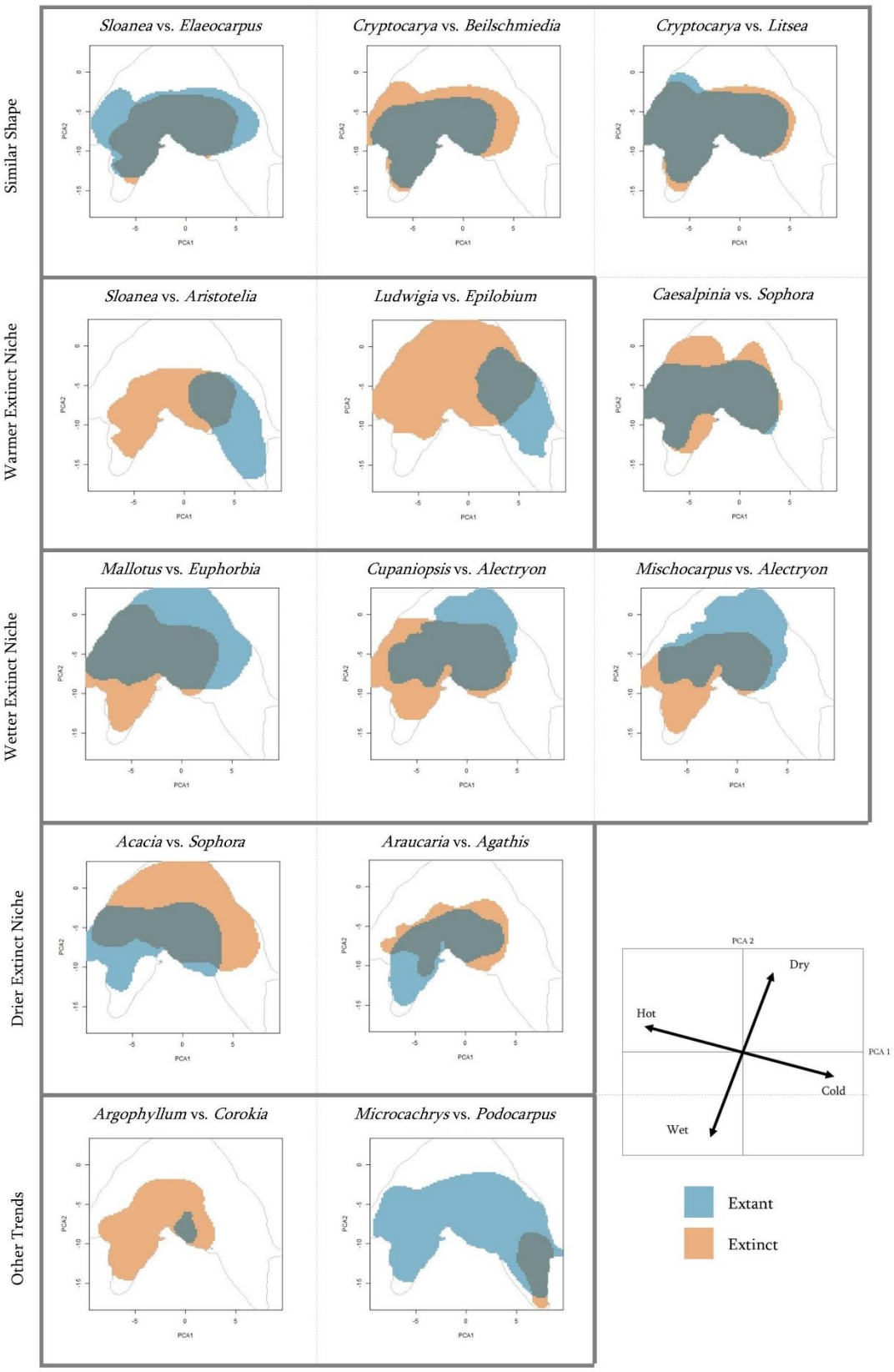


Figure 4.12: Realized climate niche of each New Zealand extant (blue) and extinct (orange) genus showing the niche overlap between genera pairs. Outline of the Australian climate space is depicted by the grey line.

In addition to the two-dimensional climate niche, the overlap of genera pairs can be compared in one dimension along each PCA axis separately to identify differences in density along both axes. The horizontal PCA axis (PCA 1) identifies areas that are hot with highly seasonal precipitation (negative) from areas that are cool with rainfall year-round (positive; Figure 4.8). Along this axis, it is hypothesized that extinct genera will be more prevalent in areas that are hot with highly seasonal precipitation (negative) because this is the most different from the current New Zealand climate (Figure 4.13).

The genera pair inhabiting the most similar area along this axis is *Caesalpinia* vs. *Sophora* and the least similar is *Microcachrys* vs. *Podocarpus*, with 76% and 15% overlap respectively (Figure 4.13). Statistically similar genera pairs are very similar along PCA 1 with an average density overlap of 51% (Figure 4.13). Non-similar genera pairs are less similar along PCA 1 with an average overlap of 26% (Figure 4.13).

For five of the eleven genera pairs with different climate niches, extant genera typically inhabit areas that are cooler with year-round rainfall. Extinct genera therefore have a climatic preference for warm and seasonally rainy areas which is consistent with the hypothesized trend (Figure 4.13). This is seen in genera pairs with overall trends of warmer or wetter extinct niches (Figure 4.13). For two of the eleven genera pairs with different climate niches, extant genera occupy a similar range of climates along PCA 1 but are more abundant in areas that are warmer with more consistent precipitation (Figure 4.13). This is seen for those genera pairs that have a drier and slightly cooler extinct niche. The genera pairs *Argophyllum* vs. *Corokia* and *Microcachrys* vs. *Podocarpus* both have one genus which is highly concentrated and fully intersects with the other genus along this axis (Figure 4.13). Therefore, although the two genera overlap in climatic preference in terms of temperature and precipitation seasonality, *Corokia* and *Microcachrys* inhabit only a small range of these variables. For *Corokia* this area overlaps with high density in *Argophyllum* contributing to niche similarity but for *Microcachrys* this area is outside the densest portion of the *Podocarpus* distribution contributing to niche difference (Figure 4.13 and Table 4.2). The genera pair *Caesalpinia* vs. *Sophora* does not show a trend in climatic preference for temperature and precipitation seasonality

between the two genera with the distributions of both genera occupying similar density and range (Figure 4.13).

The vertical PCA axis (PCA 2) is associated with a gradient from areas that are wet with consistent year-round temperatures (negative) to areas that are dry with large differences in seasonal temperatures (positive, Figure 4.8). Along this axis, it is hypothesized that extinct genera will be more prevalent in areas that are dry with large differences in seasonal temperatures because these features less common in New Zealand (Figure 4.1).

The genera pair with the most similar climatic preference along this axis is *Sloanea* vs. *Elaeocarpus* and the least similar is *Microcachrys* vs. *Podocarpus*, with 77% and 16% overlap respectively (Figure 4.13). Both statistically similar and non-similar genera pairs are more similar in terms of overall precipitation and temperature seasonality (PCA 2) than with temperature and precipitation seasonality (PCA 1). Genera pairs occupying similar climate niches have an average density overlap of 59% along PCA 2 while non-similar genera pairs have an average overlap of 37% (Figure 4.13).

For four of the eleven genera pairs with different climate niches, the extant genus inhabits areas that are wetter with more seasonally consistent temperatures than extinct genera which is consistent with the hypothesized trend (Figure 4.13). However, this trend is not pronounced in any of the pairs and is seen mostly in pairs with a warmer extinct niche and a drier and slightly cooler extinct niche (Figure 4.13). For four of the eleven genera pairs with different climate niches this pattern is reversed and more pronounced, with extant genera occupying areas that are distinctly drier with larger differences in seasonal temperatures, the opposite to the expected trend (Figure 4.13). This is seen in those genera pairs that have a wetter extinct niche and for *Microcachrys* vs. *Podocarpus*. The remaining five genera pairs have similar distributions of density and range along PCA 2 and do not show any consistent differences (Figure 4.13).

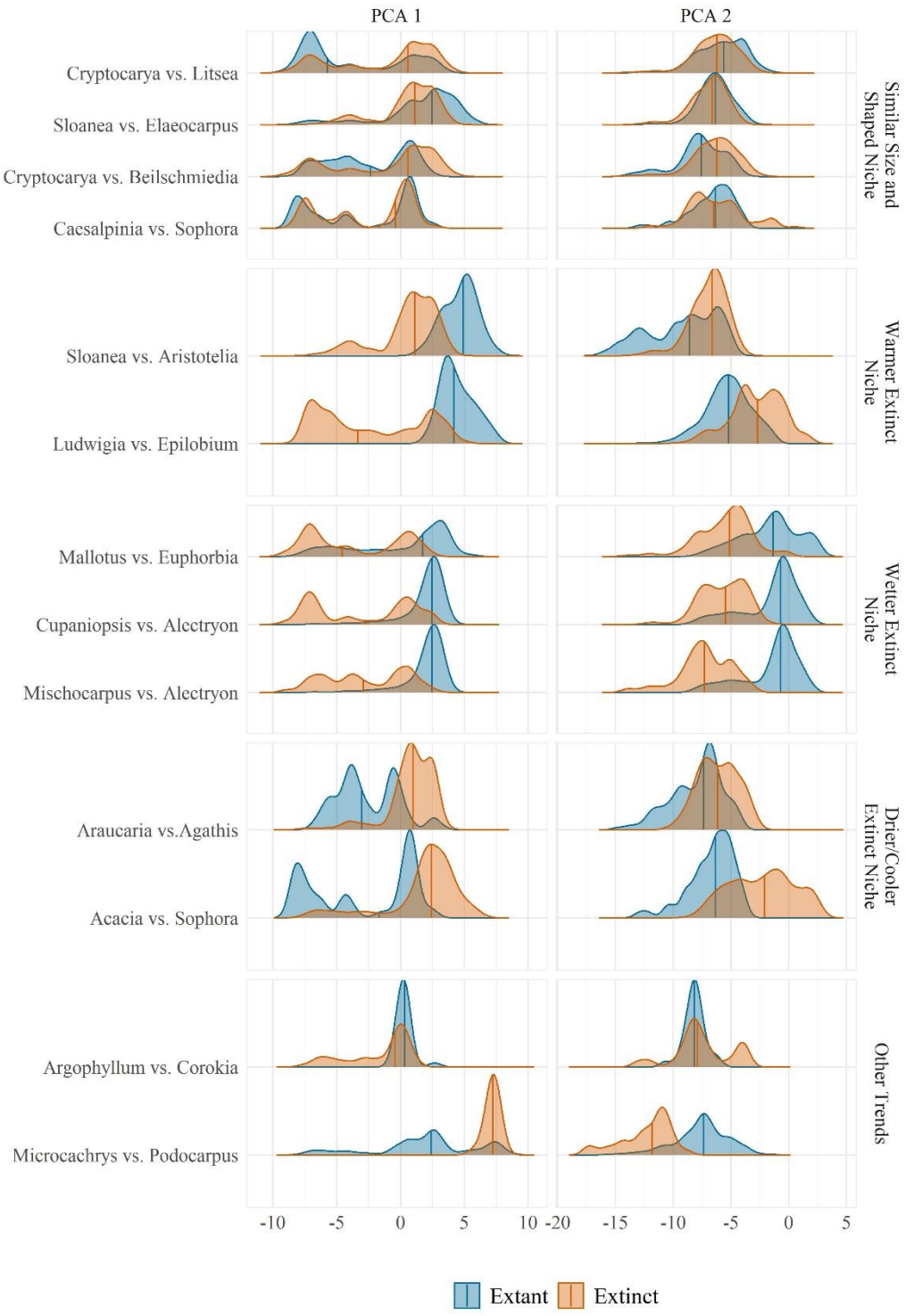


Figure 4.13: Distribution along the horizontal principle component analysis axis (PCA 1) and the vertical principle component analysis axis (PCA 2) for Australian climate space with extant (blue) and extinct (orange) genera showing overlap of genera pairs. PCA 1 is associated with a gradient from areas that are hot with highly seasonal precipitation (negative) to areas that are cool with rainfall year-round (positive). PCA 2 is associated with a gradient from areas that are wet with consistent year-round temperatures (negative) to areas that are dry with large differences in seasonal temperatures (positive). The vertical line indicates median value. Genera pairs are ordered from the highest Schoener's D (top) to the lowest (bottom).

The time of extinction from New Zealand during the Cenozoic may influence factors controlling extinction. For example, Oligocene and Miocene extinctions were associated with relatively small declines in temperature compared to those experienced during Pleistocene climate cycles. It was predicted that genera pairs with a more recent extinction would have more overlap than older extinctions because the current New Zealand climate is more similar to the climate in the relatively recent Pliocene rather than distant Eocene past. However, no trend is seen between presumed extinction date and level of climate niche overlap between extinct/extant genera in Australia ($r^2 = 0.005$, Figure 4.14). Additionally, no trend is seen between the types of niche difference and the age of extinction with multiple types of niche difference occurring during similar time periods (Figure 4.14).

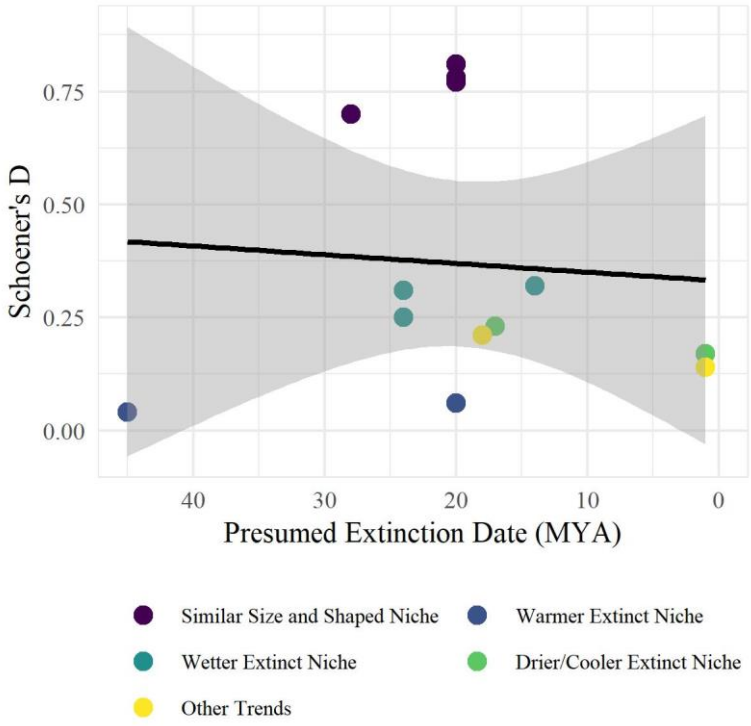


Figure 4.14: Trend between climate niche overlap in Australia (Schoener's D) and presumed New Zealand extinction timing per genus with trend line (black line, slope =0.0019, $r^2 = 0.005$) and standard error (grey shading).

4.3.4 Individual Climate Variables

In order to determine the importance of individual climate variables in contributing towards niche differences between extinct and extant New Zealand genera, kernel density overlap of each genera pair for all climate variables was analysed and compared. Climate variables that are highly similar have likely not affected extinction. Conversely, climate variables that are highly different may contribute to extinction because only one genus, either extinct or extant, occupies those areas. Genera pairs with similar climate niches (similarity p-value <0.05) have higher kernel density overlap for all variables than pairs with different climate niches (similarity p-value >0.05) with an average median overlap of 57% and 38% respectively (Figure 4.15).

For genera pairs inhabiting different climate niches, winter temperatures (bio 6 and bio 11), summer precipitation (bio 18), and temperature seasonality (bio 2 and bio 7) have the lowest median overlap between pairs and thus contribute highly to differentiating between genera pairs (Figure 4.15). However, the directionality of these differences is not consistent. For some pairs, extinct genera are greater (warmer and wetter extinct niche trends) and some are less (cooler/drier and other trends; Figure 4.16) than their extant pairs. Large differences are seen in the amount of summer precipitation (bio 18) between genera, but extinct genera that show warmer and wetter niches have more summer precipitation than extant niches. Extinct genera that are drier and cooler have less summer precipitation than their extant counterparts (bio 18, Figure 4.16).

For those genera pairs with different climate niches, both the extinct and extant genera inhabit areas with similar dry season temperature and precipitation (bio 9, bio 14, and bio 17) and annual precipitation (bio 12), making it difficult to identify the climate difference between pairs (Figure 4.15). A similar pattern is seen with these variables with extinct genera having both more and less precipitation than their extant counterpart depending on the genera pair (Figure 4.16).

For climatically similar genera pairs, temperature seasonality (bio 2 and bio 7) and dry and cold season precipitation (bio 14, bio 17, and bio 19) have the highest overlap between genera pairs (Figure 4.15). The largest difference in overlap between climatically similar and non-similar genera pairs is temperature seasonality (bio 2, bio 4, and bio 7)

and winter temperature (bio 6 and bio 11), suggesting that these variables are particularly important in accounting for the difference between pairs and may be an important indicator of the extinction events (Figure 4.15 and Figure 4.16).

Overall, there is no single climate variable that is overwhelmingly more influential than others in distinguishing New Zealand extinct from extant genera in Australian climate space. Even when one climate variable has a high median overlap the trend is not consistent between genera pairs.

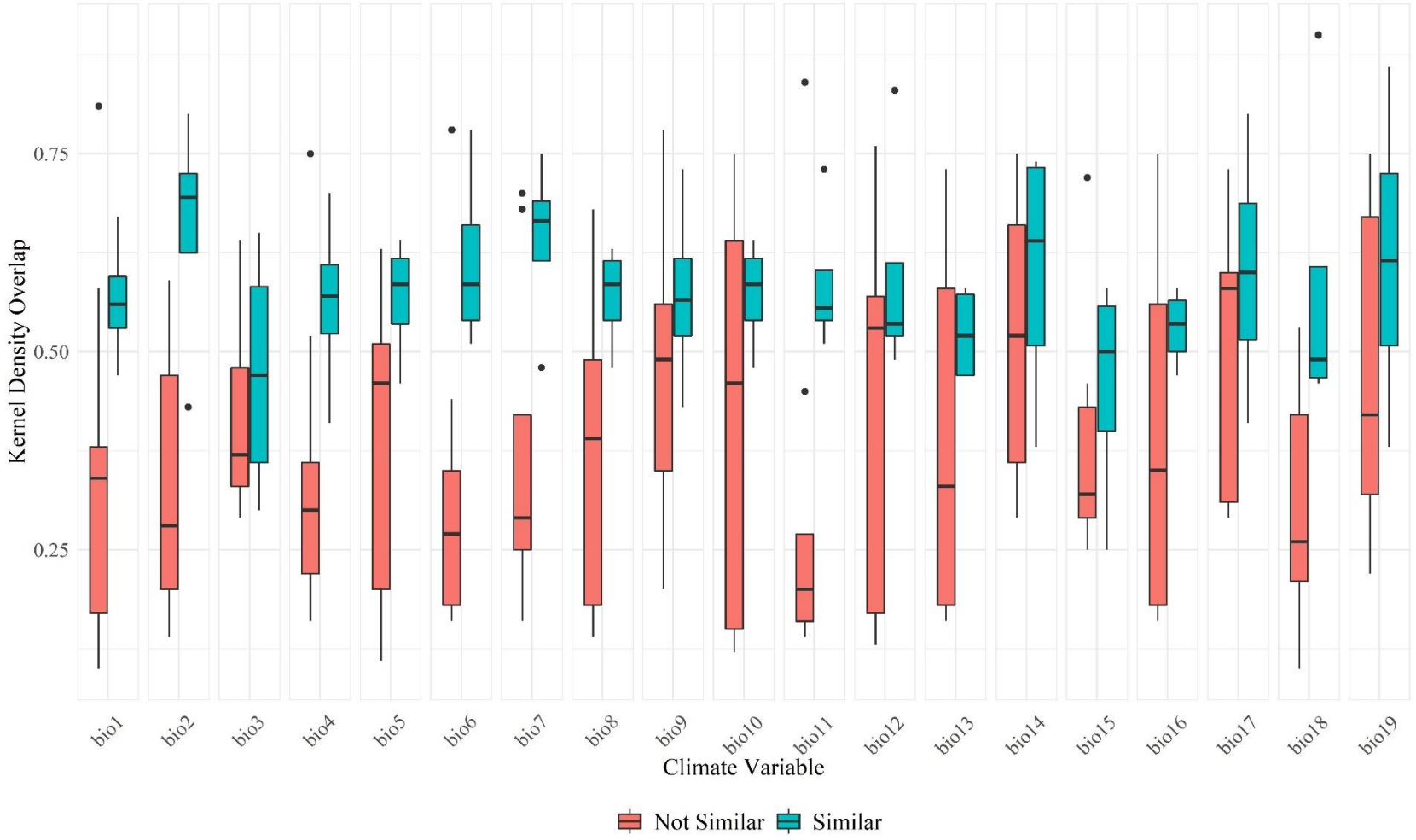


Figure 4.15: Summary of kernel density overlap for each climate variable between not similar (similarity p-value >0.05) and similar (similarity p-value <0.05) genera pairs (New Zealand extinct versus extant genera in Australian climate space).

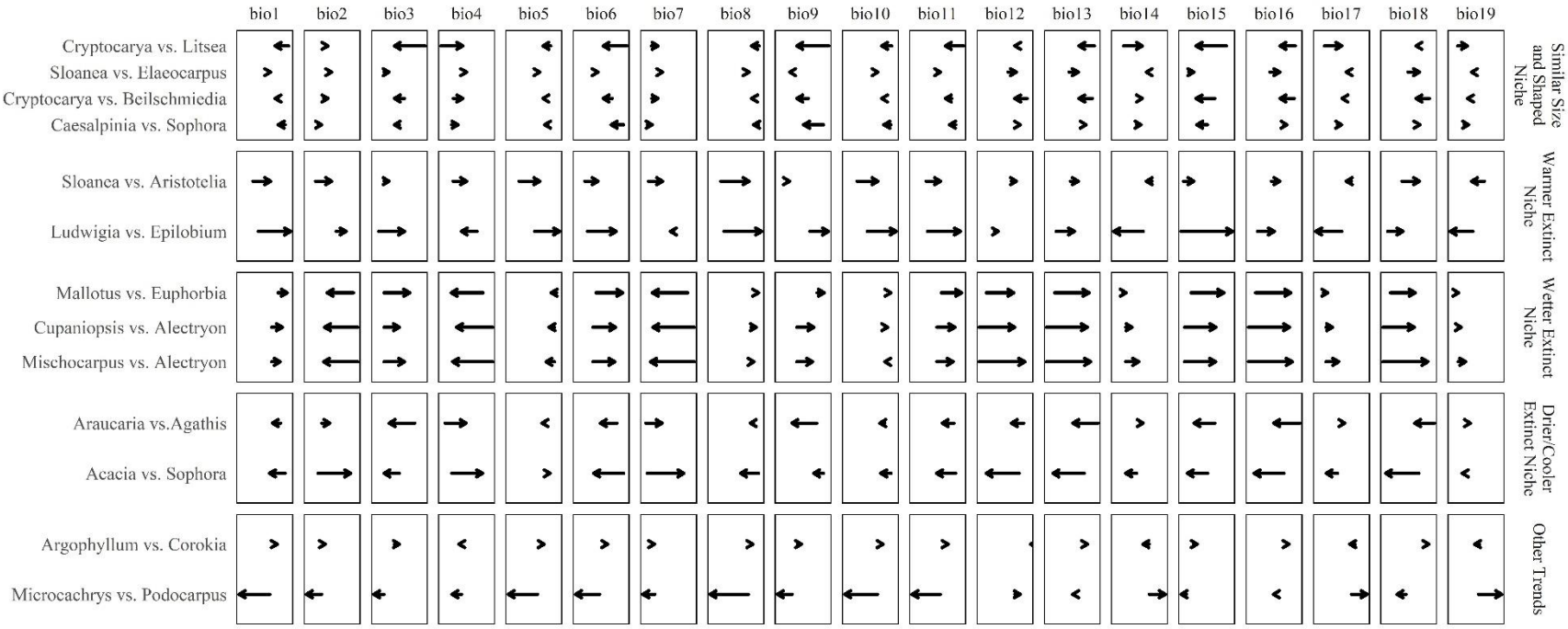


Figure 4.16: Directionality of difference for each climate variable displayed as a line from the median density of the extant genera to the median density of the New Zealand extinct genera in Australian climate space. Left facing arrows indicate that the median density of the extinct genera is less than that of the extant genera and vice versa. Line length is correlated with the difference in median values of the extinct and extant genera with longer lines indicating a greater difference between genera.

4.4 NICHE DIVERGENCE OF NEW ZEALAND EXTANT GENERA

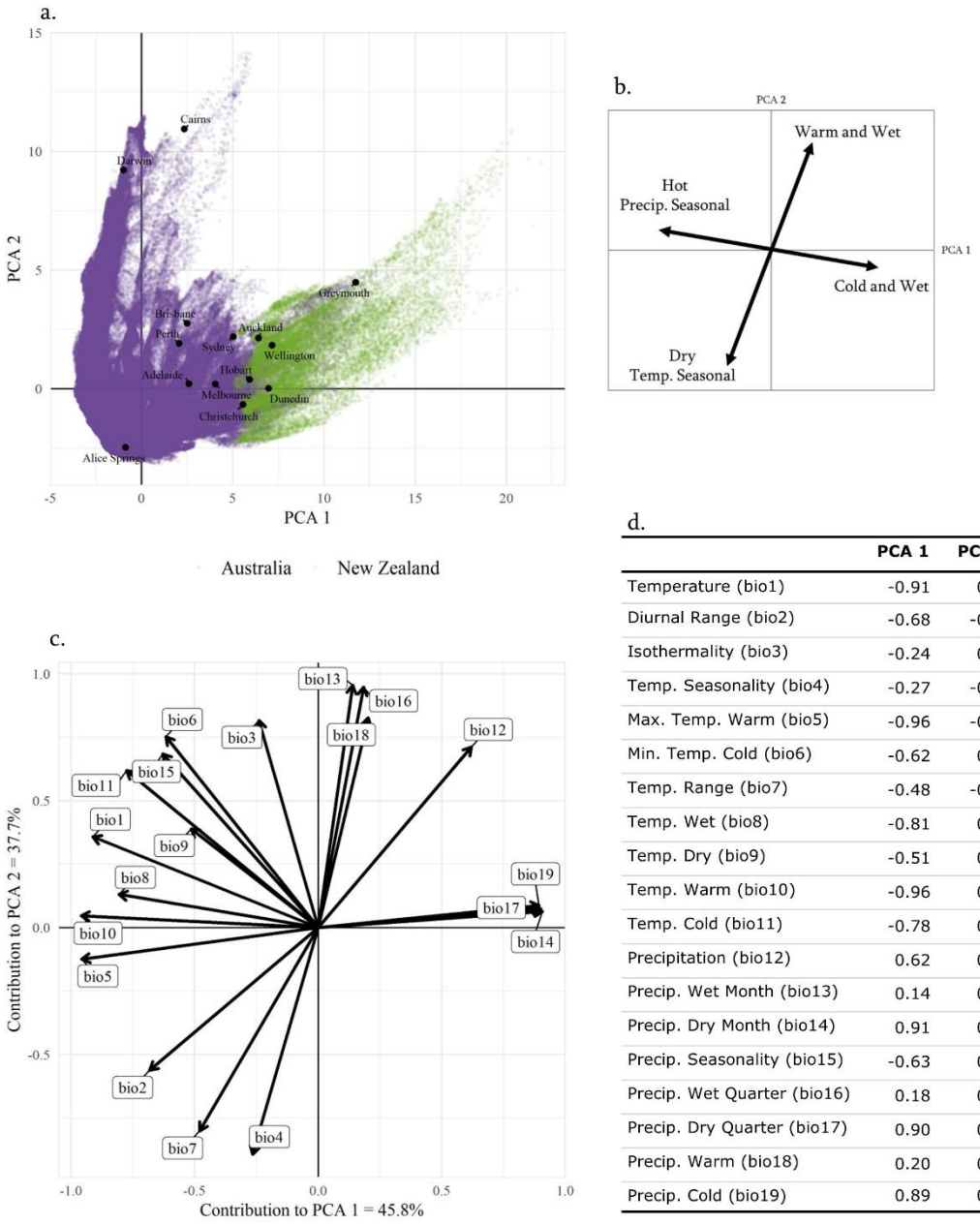
Large differences between the climate niche of the New Zealand and Australian distributions of the same genus is hypothesized to indicate that genera have undergone niche differentiation since geographic separation approximately 80 MYA or subsequent colonization. This can be determined by comparing the climate niche of genera who have distributions in both New Zealand and Australia. This section provides a description of the principle component analysis (PCA), the relative volume of each distributions' climate niche, the niche overlap between genus pairs, and the impact of individual climate variables on niche difference. In addition to comparison within the total climate space of Australia and New Zealand, niche shift within common climate space will be analysed looking specifically at niche stability, niche unfilling and niche expansion, as defined in the Section 2.2.1.

4.4.1 Australian and New Zealand Climate Space

To determine niche divergence between Australian and New Zealand distributions a PCA was completed on the combined Australian and New Zealand climate space to summarize the contributions of all nineteen climatic variables (Table 3.3; Figure 4.17). Australia and New Zealand contain diverse climates, ranging from hot and dry in central Australia to cold and wet in southwest New Zealand. The principle component analysis (PCA) of the Australian and New Zealand climate space displays a horseshoe shape (Figure 4.17a) similar to that seen in the Australian climate space analysis, which indicates that a non-linear gradient exists (Wildi, 2010).

The first axis (PCA 1) is negatively correlated with temperature variables such as average annual temperature (bio 1) and temperature of warm seasons (bio 5 and bio 10) and positively correlated with dry and cold season precipitation (bio 14, bio 17, and bio 19, Figure 4.17c and d). Overall, PCA1 explains 45.8% of the variation in the data. The second axis (PCA 2) is negatively correlated with temperature seasonality (bio 4 and bio 7) and positively correlated with warm season precipitation (bio 18) and maximum precipitation (bio 13 and bio 16, Figure 4.17c and d). Overall, PCA2 explains 37.7% of the variation in the data. This two-dimensional PCA explains 83.5% of the variation in the climate data.

The bottom left portion of the PCA is associated with dry areas that have high temperature seasonality, typified by the town of Alice Springs in central Australia (Figure 4.17a and b). The upper left portion of the PCA is associated with areas that are warm and wet with high precipitation seasonality, typified by the towns of Cairns and Darwin in north and northeast Australia (Figure 4.17a and b). The centre portion of the PCA is characterized by moderate temperatures and moderate precipitation including the towns Brisbane, Perth, Adelaide, Melbourne, and Sydney (Figure 4.17a and b). Low values on PCA 1 indicates climates are warm and dry and as values increase the climate becomes cooler and wetter, moving from Australian-only to common Australian and New Zealand climate space (Figure 4.17a). The cool and wet climate of Hobart in Tasmania is the only major Australian town to occur in both Australian and New Zealand climate space (Figure 4.17a). Many New Zealand towns occupy climate on the warmest edge of the New Zealand climate space including Auckland, Wellington, Dunedin, and Christchurch (Figure 4.17a and b). The New Zealand climate space extends to cooler and wetter climates along PCA 1 typified by towns such as Greymouth along the west coast of New Zealand (Figure 4.17a and b).



d.

	PCA 1	PCA 2
Temperature (bio1)	-0.91	0.36
Diurnal Range (bio2)	-0.68	-0.56
Isothermality (bio3)	-0.24	0.82
Temp. Seasonality (bio4)	-0.27	-0.89
Max. Temp. Warm (bio5)	-0.96	-0.12
Min. Temp. Cold (bio6)	-0.62	0.75
Temp. Range (bio7)	-0.48	-0.80
Temp. Wet (bio8)	-0.81	0.13
Temp. Dry (bio9)	-0.51	0.39
Temp. Warm (bio10)	-0.96	0.05
Temp. Cold (bio11)	-0.78	0.62
Precipitation (bio12)	0.62	0.71
Precip. Wet Month (bio13)	0.14	0.95
Precip. Dry Month (bio14)	0.91	0.06
Precip. Seasonality (bio15)	-0.63	0.68
Precip. Wet Quarter (bio16)	0.18	0.95
Precip. Dry Quarter (bio17)	0.90	0.07
Precip. Warm (bio18)	0.20	0.83
Precip. Cold (bio19)	0.89	0.09

Figure 4.17: Results from the principle component analysis (PCA) used to define New Zealand and Australian climate space. This includes a) the distribution of New Zealand and Australian climate space in two dimensions, b) a conceptual diagram showing the general changes in climatic variables seen in New Zealand and Australian climate space, c and d) the degree and direction to which each climate variable contributes to each PCA axis. PCA axis 1 explains 45.8% of the variance in points and PCA axis 2 explains 37.7% of the variance.

4.4.2 Extant Genera Niche Size in New Zealand and Australia

Climate niche volume is calculated as the proportion of available climate space occupied by the genus. Niche volume is calculated as the niche overlap (Schoener's D) of the climate niche of each distribution within the total New Zealand and Australian climate space and ranges from 0.02 (*Corokia* Australian distribution) to 0.31 (*Epilobium* New Zealand distribution) with an average niche volume of 0.18 (Figure 4.18). For most genera, the niche volume differs between their New Zealand and Australian distributions, meaning that one distribution occupies a larger range of climates than the other. This is seen for the genera *Corokia, Epilobium,* and *Aristotelia* which have much larger niches in New Zealand than Australia (Figure 4.18). Conversely, *Agathis*, *Euphorbia*, *Beilschmiedia*, *Litsea*, and *Alectryon* have a larger Australian niche (Figure 4.18). The remaining genera of *Elaeocarpus*, *Sophora*, and *Podocarpus* have similar climate niche volume between distributions (Figure 4.18).

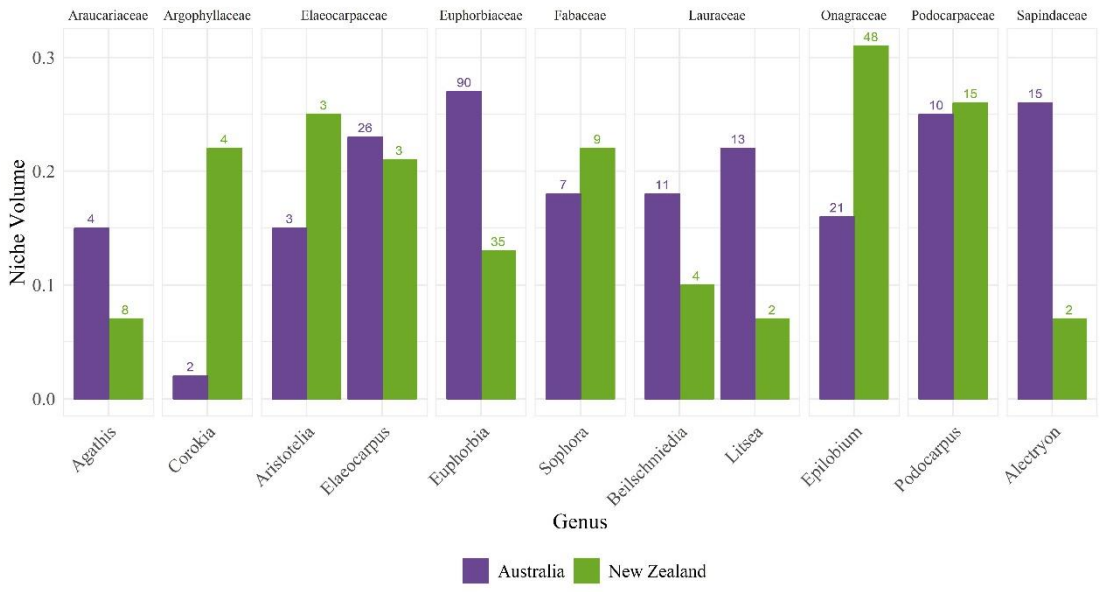


Figure 4.18: Climate niche volume for each genus occurring in Australia and New Zealand. Niche volume is calculated as the niche overlap (Schoener's D) of each genus in the total Australian and New Zealand climate space and ranges between 0-1. Numbers indicate the number of species for each genus in each region.

Climate niche volume also varies with the number of species within each genus. It is expected that the greater species richness would expand climate niche volume. For most genera, distributions with the higher species number also has a larger niche volume. For instance, *Litsea* has 13 species in Australia and 2 species in New Zealand with niche volumes of 0.44 and 0.07 respectively (Figure 4.18). However, some genera do not show

this pattern. For example, *Agathis* has 4 species in Australia and 8 species in New Zealand although it has a smaller niche volume in New Zealand than in Australia, 0.07 and 0.15 respectively (Figure 4.18). Additionally, some genera with similar niche volume have large differences in species number. For example, *Elaeocarpus* has similar niche volume between the two countries but the Australian distribution has 26 species while New Zealand only has 3 species (Figure 4.18). Overall, there is a positive trend between species number and climate niche volume for both New Zealand and Australian distributions (Figure 4.19a). However, the regression only provides a moderately good representation of the data, with r^2 values of 0.21 (Figure 4.19a). No correlation is seen between the difference in species number and the difference in niche volume between genera pairs ($r^2 = 0.04$; Figure 4.19b).

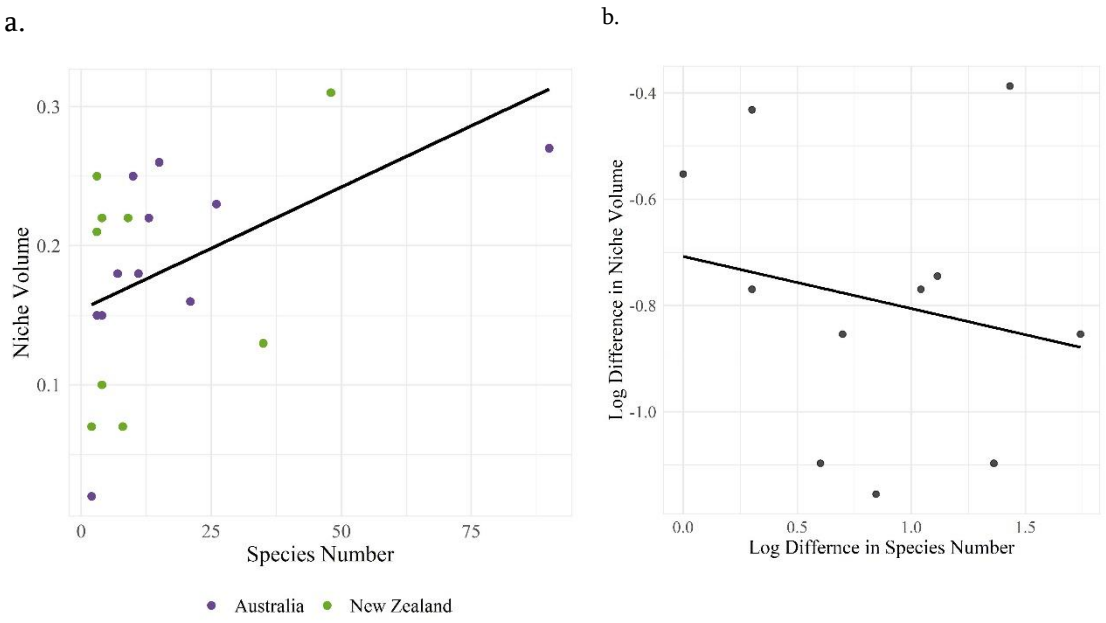


Figure 4.19: Trend between climate niche volume and the number of species per genus in Australia and New Zealand. Niche volume is calculated as the niche overlap (Schoener's D) of each genus within the combined Australian and New Zealand climate space. a) Displays the relationship between niche volume and number of species for all genera ($r^2 = 0.21$). b) Displays the relationship between the difference in niche volume compared to the difference in species number between pairs ($r^2 = 0.04$).

Overall, New Zealand distributions have a broader range of niche volumes than Australian distributions, with Australian distributions having mostly higher niche volumes (Figure 4.20). One exception to this is the genus *Corokia* whose Australian distribution has the smallest volume (outlying point in Figure 4.20). However, genera

overall have similar niche volume in Australia and New Zealand (p-value = 0.67 two-tailed t-test; Figure 4.20).

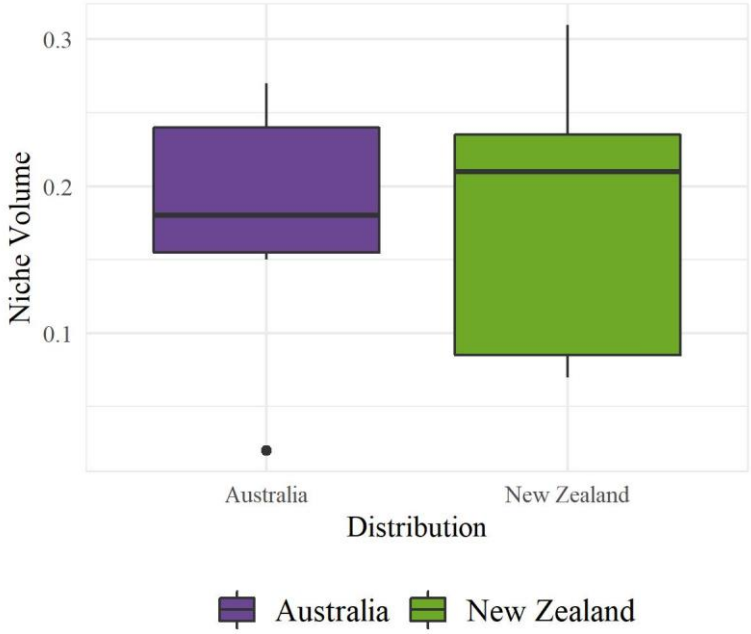


Figure 4.20: Distribution of niche volume for the Australian and New Zealand distributions, horizontal line indicates the median volume. Shows no significant difference in climate niche volume between the New Zealand and Australian distributions of each genera (p-value = 0.68, two-tailed t-test). Niche volume is calculated as the niche overlap (Schoener's D) of each genus distribution within its corresponding climate space.

4.4.3 Niche Difference between New Zealand and Australian Distributions

In order to determine niche differences in the New Zealand and Australian distribution of the same genus, the climate niche of each distribution is analysed. If climate niches differ between the two regions, then it is likely that niche change has occurred, which demonstrates climate plasticity within taxonomic groups. This is determined using the niche overlap (Schoener's D) of the Australian and New Zealand distributions. Only a portion of the Australian climate space overlaps with the New Zealand climate space (22 percent of the total climate space; overlapping grey outlines in Figure 4.21). Therefore, dynamics within the common New Zealand and Australian climate space (referred to herein as common climate space) are important indicators of the type and extent of niche shift and were included in the study.

Climate niche differences between genus pairs were used to identify the type of climate evolution in the two countries. Most Australian climate niches range from wet and warm to cooler but still wet (Figure 4.21). The Australian climate niches of two genera, *Euphoribia* and *Alectryon*, extend into areas that are dry with highly seasonal temperatures (lower left of climate space; Figure 4.21). The Australian distributions of the genera *Aristotelia* and *Epilobium* are restricted to the cooler and wetter parts of the Australian climate space (Figure 4.21). The New Zealand distributions of the genera are typically concentrated along the warmest and wettest edge of the New Zealand climate space (left and top edge of New Zealand climate space; Figure 4.21). However, most genera do not extend fully to the warmest edge of the New Zealand climate space (left edge of New Zealand climate space; Figure 4.21).

Many of the New Zealand distributions for these genera inhabit climates primarily within the common climate space and most of the climates associated with their distribution are available geographically in Australia. The average overlap of the genera's New Zealand niches with this common climate space is large (77 percent) with a few exceptions (Table 4.3, Figure 4.21). The opposite is seen for the Australian distributions which characteristically have only small portions of their niche within common climate space, occupying a substantial number of climates outside what is common with New Zealand (Table 4.3, Figure 4.21). Overall, the average overlap of the Australian niche with common climate is small (31 percent) with a few exceptions (*Aristotelia* and *Epilobium*; Table 4.3, Figure 4.21).

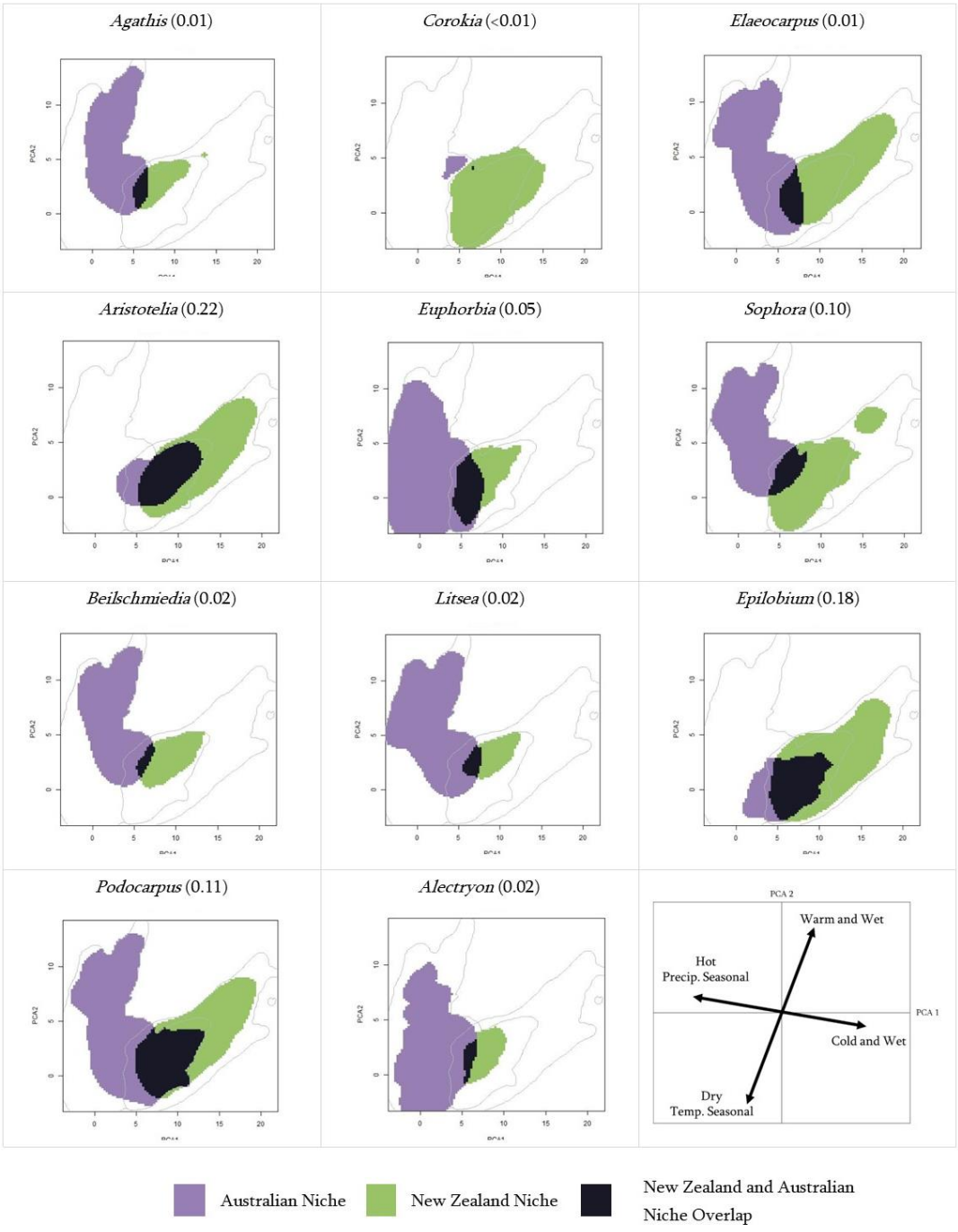


Figure 4.21: Realized climate niche of each Australian (purple) and New Zealand (green) distribution for each genus showing the climate niche overlap. Outline of the Australian and New Zealand climate space is depicted by the grey lines. Schoener's D value measuring the difference in New Zealand and Australian climate space is stated for each pair.

Table 4.3: Percent of total climate niche of each distribution that occurs within the common climate space in Australia and New Zealand.

Genus	Percent of Niche in Common Climate Space	
	New Zealand	Australian
Agathis	94%	15%
Corokia	77%	2%
Elaeocarpus	53%	27%
Aristotelia	50%	94%
Euphorbia	98%	20%
Sophora	78%	16%
Beilschmiedia	97%	14%
Litsea	98%	17%
Epilobium	55%	78%
Podocarpus	50%	39%
Alectryon	99%	16%
Average	**77%**	**31%**

All but one genus extends into the common climate space of Australia and New Zealand. The only distribution which exists almost entirely outside of the common climate space is the Australian distribution of *Corokia,* having very little overlap with its New Zealand counterpart (Figure 4.21). Most of the Australian distributions do not extend substantially into the common climate space while many of the New Zealand distributions do extend into the common climate space (Figure 4.21). For example, the Australian distribution of *Podocarpus* extends to the boundary of the Australian climate space and covers most of the common climate space (Figure 4.21). To a lesser extent the Australian distributions of *Epilobium* and *Aristotelia* also extend substantially into the common climate space (Figure 4.21 and Table 4.3).

In contrast most New Zealand distributions do not extend to the edge of the New Zealand climate space and most niches do not occupy the warmest portion of the New Zealand climate (Figure 4.21). The New Zealand distributions which occupy the fullest amount of the common climate space are *Corokia* and *Sophora*, however this does not lead to high niche overlap with Schoener's D values of 0.0 and 0.1 respectively (Figure 4.21). For all genera there are portions of the common climate space that are occupied by one distribution and not the other (Figure 4.21).

In addition to the two-dimensional niche overlap, genera distribution climate niches are also compared in one dimension along individual PCA axis. The horizontal PCA axis (PCA 1) is associated with a gradient from areas that are hot with highly seasonal precipitation (negative) to areas that are cool with rainfall year-round (positive; Figure 4.22). The PCA 1 axis has low overlap between the two countries (2 percent, Figure 4.22). Overlap along this axis for the different genera distributions is also low, averaging 8 percent (Figure 4.22).

Along PCA 1 only one genus has high overlap between distributions (*Aristolelia*; Figure 4.22). The two distributions of *Aristolelia* occupy more similar areas in terms of temperature and precipitation seasonality than the other genera in similar comparisons. *Epilobium* and *Podocarpus* also have higher than average overlap (17 percent for both pairs). However, these pairs show distinct differences in density along PCA 1, with the Australian peak occurring in areas that are hotter with more seasonal rainfall than the New Zealand peak (Figure 4.22). For all pairs except *Aristolelia*, the peak density in the Australian distribution occurs in areas that are hotter with more seasonal rainfall and fall either within New Zealand climate space or at the point in which the Australian and New Zealand climate space begin to overlap (Figure 4.22). Alternatively, the peak density of the New Zealand distributions occurs within the common Australian and New Zealand climate space for all genera (Figure 4.22).

The vertical PCA axis (PCA 2) is associated with a gradient from areas that are dry with large differences in seasonal temperature (negative) to areas that are wet with only moderate seasonal temperature changes (positive; Figure 4.17). The PCA 2 axis has high overlap between the two countries (39 percent, Figure 4.22). However, the peaks of Australia and New Zealand along PCA 2 are separated with genera in Australia mostly occupying areas drier with larger differences in seasonal temperature than New Zealand (Figure 4.22). Overlap along this axis for genera is also high, averaging 34 percent (Figure 4.22). There is also less overall difference between the climate niche in Australia and New Zealand, with most distributions occurring in the wetter and more temperate areas.

Along PCA 2 there are two main trends. This first trend is for New Zealand distributions that peak in climates that are drier with larger differences in seasonal temperature than the Australian distribution which is contrary to the overall trend between the two countries (Figure 4.22). This trend is seen for *Agathis, Corokia, Sophora, Belischmiedia*, and *Litsea* (Figure 4.22). The second trend is for New Zealand distributions that peak in climates that are wetter and more temperate than the Australian distribution, which is consistent with the overall trend between the two countries (Figure 4.22). This pattern is seen for *Elaeocarpus, Aristotelia, Euphorbia, Epilobium*, and *Alectryon* (Figure 4.22). One genus, *Podocarpus*, has high overlap with both distributions peaking at approximately the same climatic point suggesting no difference in niche along this axis (Figure 4.22).

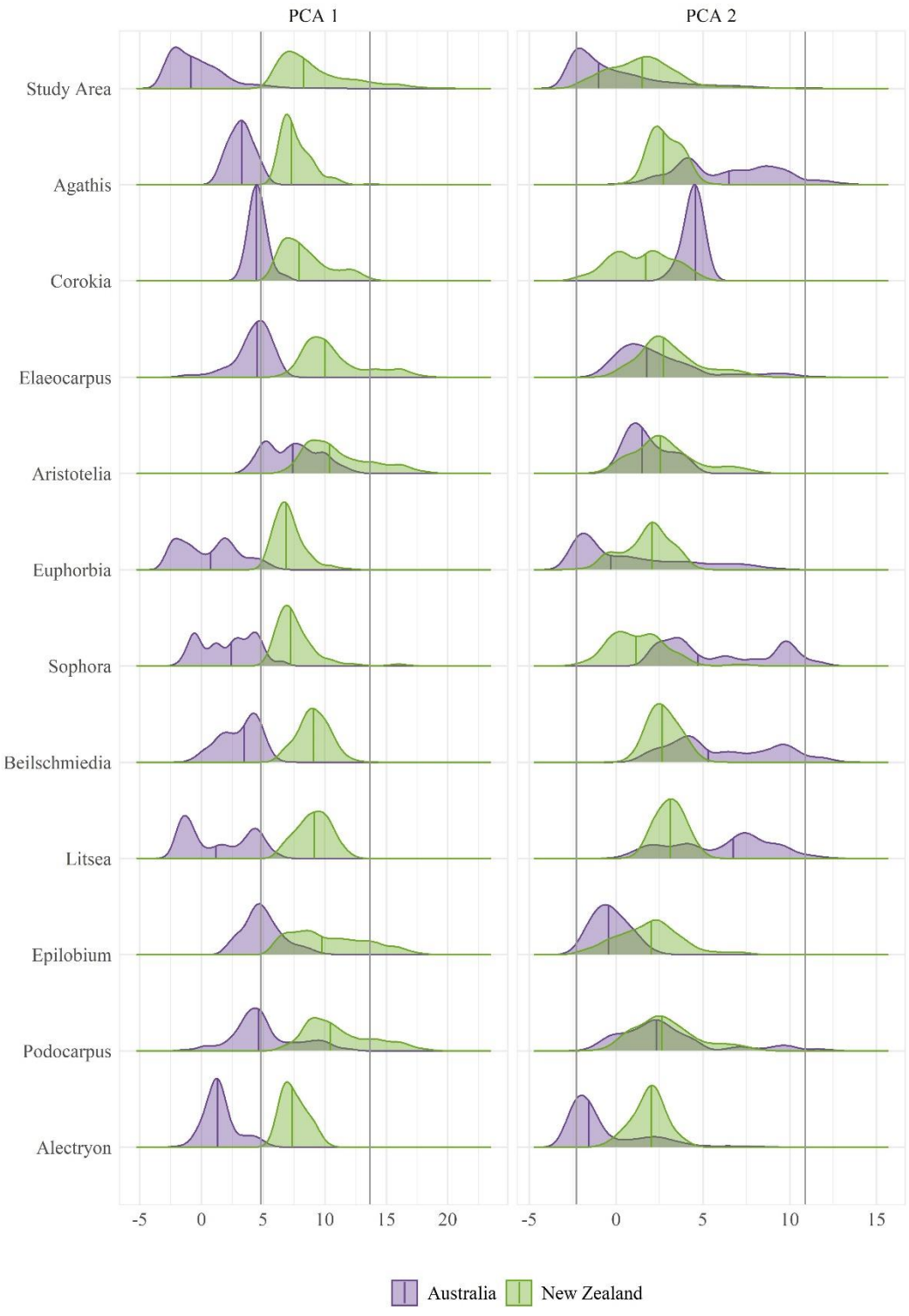


Figure 4.22: Density of occurrence along vertical principle component analysis axis (PCA 1) and the horizontal principle component analysis axis (PCA 2) for the Australian (purple) and New Zealand (green) distributions of each genus. PCA 1 ranges from areas that are hot with highly seasonal precipitation (negative) to areas that are cool with rainfall year-round (positive). PCA 2 ranges from areas that are dry with large differences in seasonal temperature (negative) to areas that are wet with only moderate seasonal temperature changes (positive). Between vertical lines is overlapping climate space common between Australian and New Zealand.

Climate niche overlap of the Australian and New Zealand distributions of extant New Zealand genera are low and range from <0.01 (*Corokia*) to 0.22 (*Aristotelia*) with an average niche overlap of 0.07 when accounting for difference in climate (Table 4.4, see Section 3.2.2 for details on this test). Of the eleven genera, eight genera were statistically similar between distributions, when accounting for difference in climate (p-value < 0.05, Table 4.4). However, the low overlap between climate spaces of the two countries may limit valid comparisons using this metric with the effect of low overlap in available climate not being explicitly explored in literature. This effect is seen in the overlap values decreasing and none of the genera being statistically similar between distributions when differences in available climate are not accounted for in calculating Schoener's D and the similarity metric (Table 4.4, see Section 3.2.2 for details on these tests).

Table 4.4: Results of climate niche overlap between genera distributions in New Zealand and Australian distributions. Includes Schoener's D metric of niche overlap (0 = no overlap, 1 = full overlap) and similarity test accounting for (Climate Accounted) and not accounting for (Climate Not Accounted) the differences in climate space between New Zealand and Australia. Similarity test calculates a significance value for one distribution predicting the niche of the other distribution (p-value, - = not significant, * = <0.05, ** = <0.01). Similarity test is directional, results are displayed for each direction.

Family	Pair	Climate Accounted			Climate Not Accounted		
			Similarity			Similarity	
		Schoener's D	AUS to NZ	NZ to AUS	Schoener's D	AUS to NZ	NZ to AUS
Study Area	Australia vs. New Zealand	**0.32**	**	**	0.09	-	-
Araucariaceae	Agathis	**0.01**	*	*	0	-	-
Argophyllaceae	Corokia	**<0.01**	*	*	0	-	-
Elaeocarpaceae	Elaeocarpus	0.01	-	-	0	-	-
	Aristotelia	**0.22**	*	**	0.19	-	-
Euphorbiaceae	Euphorbia	**0.05**	*	*	0.03	-	-
Fabaceae	Sophora	**0.10**	**	*	0.07	-	-
Lauraceae	Beilschmiedia	**0.02**	*	*	0	-	-
	Litsea	0.02	-	-	0	-	-
Onagraceae	Epilobium	**0.18**	**	**	0.07	-	-
Podocarpaceae	Podocarpus	0.11	-	-	0.04	-	-
Sapindaceae	Alectryon	**0.02**	*	*	0.01	-	-

This study examined differences in the common climate space in Australasia to understand the extent to which each distribution has been conserved or diverged. If climate niche has been conserved, genera would have high overlap within the common

Australia/New Zealand climate space. If they have diverged, genera would be expected to have low overlap in the common climate space. It would also be expected that they occupy a similar proportion of the common climate space in both countries.

Within the common climate space, the Australian distribution always occupies areas that are warmer than the New Zealand distribution. Overall, New Zealand distributions occupy a greater proportion of the common climate than Australian distributions, with an average of 61 percent and 38 percent coverage respectively (Figure 4.23). This may be because common climates are more available geographically in New Zealand than in Australia. However, this does not fully explain why genera do not experience complete overlap in the common climate.

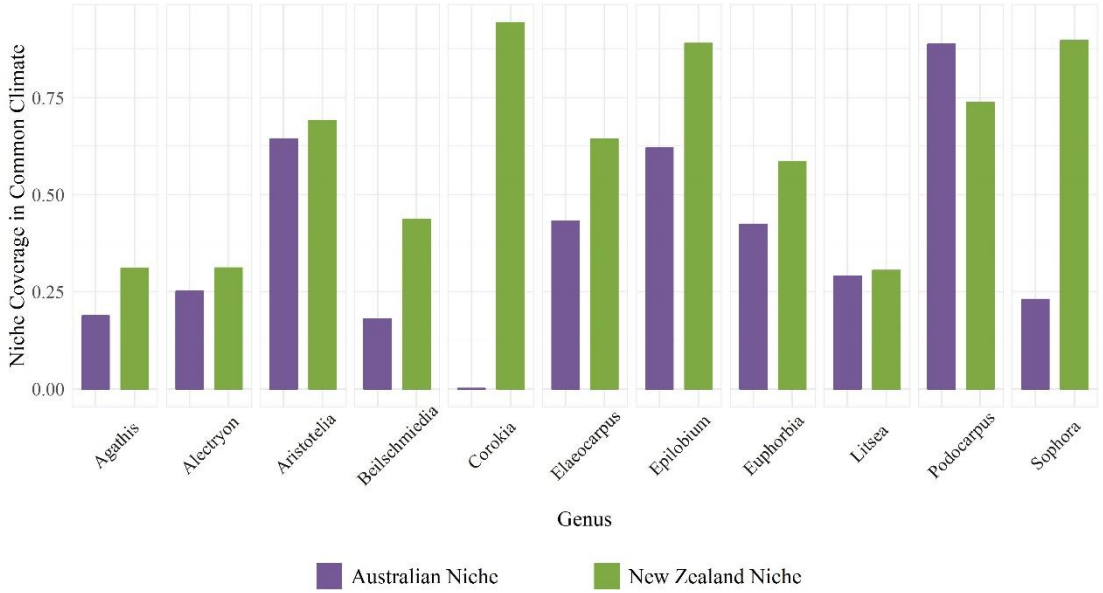


Figure 4.23: Portion of common climate space occupied by the genera in Australia (purple) and New Zealand (green).

It is also important to examine the dynamics of what climate space is occupied by each distribution within common climate space. The level of niche stability refers to the areas in common climate space that both the Australia and New Zealand distribution occupy. The genera with the highest amount of niche stability are *Podocarpus* (68 percent), *Aristotelia* (60 percent), and *Epilobium* (56 percent; Table 4.5).

However, this pattern of high niche stability is not replicated for most of the genera investigated. If there is area within the common climate space that is occupied by the New Zealand distribution but not by the Australian distribution it suggests that the

Australian distribution is not utilizing all suitable climates available to them or that the species and individuals of that genus in New Zealand have diverged climatically from their Australian counterparts, this is referred to as expansion. This is seen in all the genera, except *Podocarpus*, with the New Zealand distribution having large niche expansion on average (50 percent; Table 4.5). In contrast, the area within common climate space that is occupied by the Australian distribution and not the New Zealand distribution suggests that the New Zealand distribution is unable to inhabit those areas in New Zealand, referred to as niche unfilling. There is less niche unfilling on average (20 percent) in the common climate space (Table 4.5). This suggests that New Zealand distributions are better at occupying common climate than Australian distributions.

Table 4.5: The amount of niche stability, unfilling, and expansion within the common climate space in Australia and New Zealand. Niche stability refers to the areas in common climate space that both the Australian and New Zealand distribution occupy, unfilling refers to the areas in common climate space that only the Australian distribution occupies, and expansion refers to the areas in common climate space that only the New Zealand distribution occupies. For full definition of these metrics see Section 2.2.1.

Genus	Stability	Unfilling	Expansion
Agathis	19%	26%	55%
Corokia	0%	0%	100%
Elaeocarpus	21%	28%	51%
Aristotelia	60%	17%	23%
Euphorbia	42%	17%	40%
Sophora	20%	4%	75%
Beilschmiedia	10%	22%	68%
Litsea	16%	41%	44%
Epilobium	56%	8%	36%
Podocarpus	68%	24%	8%
Alectryon	14%	37%	49%
Average	30%	20%	50%

4.4.4 Individual Climate Variables Influencing Niche Divergence

In order to determine the importance of each climate variable in influencing niche divergence, the kernel density overlap of genera in the two distributions was determined. Climate variables with high density overlap indicate niche similarity and climate variables with low density overlap suggests niche difference. On average, the overlap is moderate with an overall median overlap of 23 percent for all climate variables combined (Figure 4.24).

Climate variables in which the New Zealand and Australian distributions were very different and may be a cause of niche divergence were primarily associated with warm season temperature (bio 5 and bio 10) and dry season precipitation (bio 14 and bio 17, Figure 4.24). In general, New Zealand distributions experienced lower temperatures than their Australian relatives for all genera except *Aristotelia* which experienced no difference between the two distributions for this variable (bio1; Figure 4.25). For dry season precipitation, the New Zealand distributions experienced greater precipitation during the dry season than their Australian relatives (bio 14 and bio 17). This suggests that New Zealand distributions do not experience precipitation as low as their Australian counterparts. Additionally, New Zealand distributions experience more winter precipitation (bio 19) and lower average temperatures (bio 1) than their Australian counterpart (Figure 4.25).

Climate variables not contributing to niche difference are associated with annual temperature range (bio 7), dry season temperature (bio 9), and wet season precipitation (bio 13 and bio 16; Figure 4.24). The medians for these variables are similar between distributions in both countries and directionality of difference is not consistent between distributions (Figure 4.25). Interestingly, five of the eleven genera have less wet season precipitation (bio 13 and bio 16) in their New Zealand distribution, which is opposite of the trend between climate space of the two countries with New Zealand experiencing more wet season precipitation than Australia (Figure 4.25). This conflicting pattern is also seen for warm season precipitation (bio 18), where the same five genera inhabit areas with less warm season precipitation than their Australian counterpart, again in contrast to the trend between the two countries with New Zealand generally experiencing more warm season precipitation than Australia (Figure 4.25). This suggests that although these variables are not large contributors to the overall difference in climate niche (due to high overall similarity), wet and warm season precipitation may be an important distinguishing characteristic for the difference in climate niche between the two distributions for *Agathis*, *Corokia*, *Sophora*, *Beilschmiedia*, and *Litsea*.

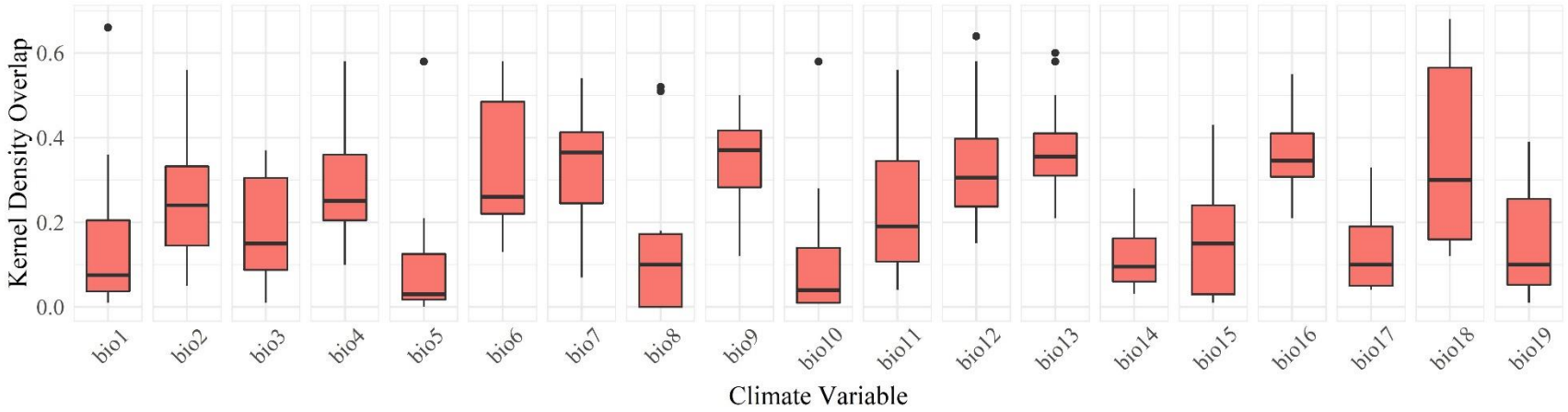


Figure 4.24: Summary of kernel density overlap for each climate variable between genera in New Zealand and in Australia.

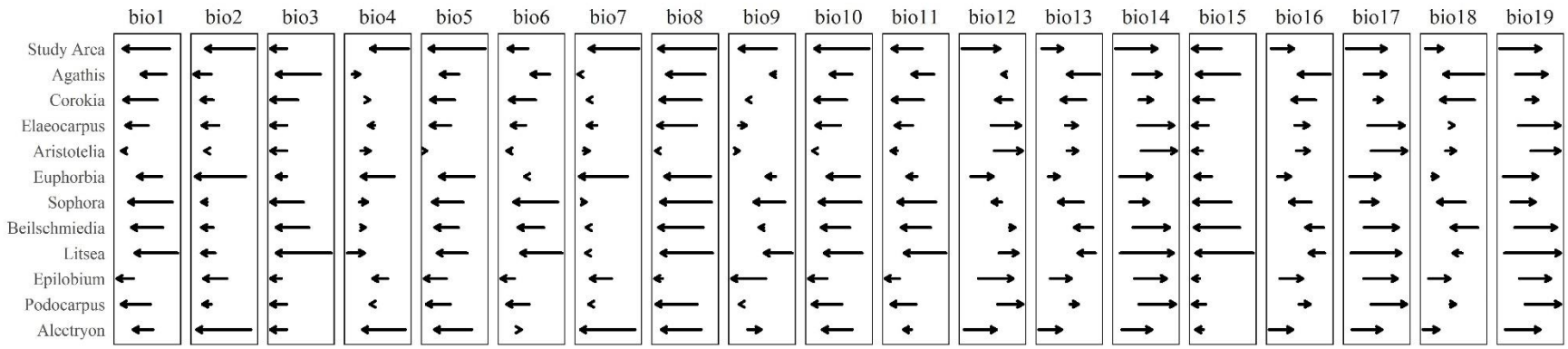


Figure 4.25: Directionality of difference for each climate variable between the New Zealand and Australian distribution of genera. Displayed as a line from the median density of the Australian distribution to the median density of the New Zealand distribution. Left facing arrows indicate that the median density of the New Zealand distribution is less than that of the Australian distribution and vice versa. Line length is correlated with the difference in median values of the distributions with longer lines indicating a greater difference between distributions.

Chapter Five

5 Discussion

The loss of many New Zealand plant genera during the Cenozoic in response to changing environments provides a novel opportunity to understand the climatic factors associated with regional extinctions. Identifying climate variables that may induce population declines and indicate extinction risk can assist conservation strategies for plant communities, which may become especially important as climate continues to change in the future. This section discusses the major results of the study, including justification for using Australian climates to understand New Zealand plant extinctions (Section 5.1), how the climates inhabited by locally extinct New Zealand genera differ from closely related extant New Zealand genera in Australia (Section 5.2), and how the climate niches of New Zealand extant genera have shifted when compared to the Australian distribution of the same genus (Section 5.3). Specifically, each section will examine how individual climate variables contribute to the overall differences seen between related taxa and contribute to extinction in New Zealand.

5.1 Analogues of Cenozoic Climate

Climates have changed throughout the history of earth with many periods providing insight into predicted future climates (Burke et al., 2018). Comparing community change, including extinctions, over time provides insight into how ecosystems have responded to environmental change in the past (Fordham et al., 2016). Direct observation of past change can be difficult, however, the substitution of space for time has been shown to

represent past changes in community composition (Blois et al., 2013). In this study, New Zealand past climates are represented in space by areas of analogous climates in Australia (Figure 4.2).

In the early Cenozoic New Zealand and Australia continued to move apart but remained at approximately the same latitude with similar climates, characterized as sub-tropical, until the Oligocene (Lee et al., 2001). During the Oligocene (30 to 25 MYA) New Zealand drifted northward and marine transgression occurred, resulting in New Zealand's smallest land area (Lee et al., 2001). Following the Oligocene, New Zealand experienced an increase in land area, further cooling climate, and mountain building during the late Miocene (Lee et al., 2001). Starting in the late Pliocene and early Pleistocene, New Zealand experienced rapid cooling coinciding with the creation of the Southern Alps resulting in drastic changes from historic climates and landscapes having a significant impact on New Zealand flora (Lee et al., 2001; McGlone et al., 2001).

Currently, both Australia and New Zealand are cooler than they were during most of the Cenozoic, except for glacial periods in the Pleistocene (Sturman and Tapper, 2006). Terrestrial temperatures in Australia during the Eocene were warmer than present with mean annual temperature (MAT) in Western Tasmania estimated at approximately 24 ^{O}C at a latitude of approximately 65 ^{O}S (Carpenter et al., 2012; Greenwood, 1994). This is compared to the current MAT of Tasmania of 10 ^{O}C at a latitude of 42 ^{O}S seen in our results (Figure 4.1). The Australian northern tropical areas are similar to those that existed across much of Australia during the Eocene and have since retreated to the most northern portions of the continent (Willis and McElwain, 2014; Mucina, 2019). Warm temperate areas developed in Australia during the Oligocene and persist in similar locations to the present day (Willis and McElwain, 2014; Mucina, 2019). Areas with drier climates also currently exist in Australia that were not seen in the past such as the deserts and dry shrubland (Willis and McElwain, 2014; Mucina, 2019).

During the Eocene, temperatures in New Zealand were estimated at up to 23 ^{O}C (Conran et al., 2016). These temperatures are up to 13 ^{O}C warmer than present day average MAT of approximately 10 ^{O}C (Figure 4.1) and are similar to those climates that currently exist

on the northeast coast of Australia (Figure 4.2). During the Oligocene and Miocene temperatures in New Zealand ranged from 18 ^{O}C to 20 ^{O}C (Prebble et al., 2017) which is approximately 8^{O}C to 10^{O}C greater than present day MAT of approximately 10 ^{O}C (Figure 4.1) and similar to those climates that currently exist on the southeast coast of Australia (Figure 4.2).

Much of New Zealand currently experiences annual precipitation ranges consistent with Cenozoic environments, with the exception of the rain shadow on the South Island which is likely more arid than any period in the Cenozoic (Table 4.1 and Figure 4.1). During the Eocene, New Zealand experienced high levels of precipitation (Conran et al., 2016) similar to current precipitation on the west coast of the South Island and the northeast coast of Australia (Table 4.1 and Figure 4.1). Through the Oligocene, Miocene, and Pliocene New Zealand was characterized by moderate precipitation of approximately 2000mm which is similar to the precipitation seen in much of present day New Zealand and parts of the east coast of Australia (Table 4.1 and Figure 4.1; Prebble et al., 2017). Precipitation increased through the Pleistocene with maximum precipitation similar to that experienced by the west coast of the South Island of New Zealand but with minimum precipitation similar to areas along much of the Australian east coast (Table 4.1 and Figure 4.1; Prebble et al., 2017).

Overall, current day New Zealand is cooler than the pre-Pleistocene past with areas of rainfall similar to all periods during the Cenozoic with the exception of novel arid climates in the rain shadow of the Southern Alps. All Cenozoic New Zealand climates, based on temperature and precipitation, are found in the Australian climate space, primarily along the east coast. These areas are suitable analogues for the full range of Cenozoic climates experienced in New Zealand and therefore ideally suited to test hypotheses regarding the extinction of select genera in New Zealand.

5.2 Climate Correlates of New Zealand Plant Extinctions

This study aimed to determine the climate niche differences of New Zealand extinct and extant genera in their current distributions, which could explain their relative susceptibility to Cenozoic climate shifts. A majority (69 percent; 9 out of 13 genera pairs) of New Zealand extinct genera occupy significantly different climate niches than their closely related extant counterpart from the same family. One additional pair has similar climate niches (high overlap), but this was not significant. Therefore, eight pairs show a climatic susceptibility indicator that may highlight why they became extinct in New Zealand. However, there are no consistent climatic factors distinguishing extinct and extant genera in each family with five major trends emerging:

- New Zealand extinct genera have warmer and drier climate niches than their extant counterparts (2 pairs),
- New Zealand extinct genera have wetter, slightly warmer, and more temperate climate niches than their extant counterparts (3 pairs),
- New Zealand extinct genera have cooler and drier climate niches than their extant counterparts (2 pairs),
- New Zealand extinct genera have cooler and wetter climate niches than their extant counterparts (1 pair), and
- New Zealand extinct genera have little difference in climate niches to their extant counterparts (5 pairs)

In this section, climatic correlates of New Zealand extinct and extant plant genera in their current Australian distributions are discussed with reference to their climate niche volume (Section 5.2.1) and specific climatic characteristics of New Zealand extinct taxa that did (Section 5.2.2) and did not (Section 5.2.3) show differences in their climate niches compared with their extant familial counterparts.

5.2.1 Climate Niche Volume

No significant difference was seen in climate niche volume between New Zealand extinct and extant genera in Australia (Figure 4.11). Therefore, it appears that the range of

climate environments occupied by extinct genera was not a predictor of extinction in New Zealand. Some extinct genera occupied a very narrow range of climates (*Microcachrys*) while others occurred across a very broad range of climates (*Acacia;* Figure 4.9). Amongst plant groups, few studies have looked at the difference in niche volume between extinct and extant taxa, and no studies could be found investigating niche volume and the extinction of plant species. However, results here are consistent with those found for extinct and extant megafauna during the Pleistocene which fail to implicate climate niche volume as a significant predictor of survival or extinction (Di Febbraro et al., 2017). The absence of a pattern was also found in a study of extinct and extant bivalve and gastropod species between the Pliocene to the present (Saupe et al., 2015).

Climate niche volume also increased with the number of species richness in a genus, with a strong trend at low species numbers which plateaued as the number of species increased above 100 species (Figure 4.10). Genera with large species numbers also have larger geographic ranges, e.g., *Acacia* and *Euphorbia*, than those with few species, such as *Microcachrys* (Figure 4.4 and Figure 4.9). It is known that taxa with larger geographic ranges have broader climate niche volumes (Granot and Belmaker, 2019; Vazquez and Stevens, 2004). However, the link between species number and niche volume is not well studied (Vazquez and Stevens, 2004). No difference was observed between the difference in climate niche volume and the difference in number of species for all genera pairs (Figure 4.10). Therefore, any difference or similarity in niche volume or shape is the result of differences in the climate niche and not differences in the species number between genera pairs.

5.2.2 Extinction Events with Climate Indicators

The climate niches of eight New Zealand extinct genera show distinct climate differences when compared to their New Zealand extant counterparts in Australia indicating potential climatic indicators of these extinction events. These genera show four distinctive trends with some extinct genera occupying warmer areas, wetter areas, cooler/drier areas, or cooler/wetter areas.

Warmer Niches

The New Zealand extinct genera generally have warmer niches than their New Zealand extant counterparts co-occurring in Australia, shown by the lowest amount of niche overlap (Table 4.2; Schoener's D of 0.06 for *Sloanea* and *Aristotelia* and 0.04 for *Ludwigia* and *Epilobium*). Both of the extinct genera, *Sloanea* and *Ludwigia,* have warmer niches than their extant counterparts (Figure 4.12; for *Sloanea* this only applies when compared to *Aristotelia*, for discussion of *Sloanea* and *Elaeocarpus* see Section 5.2.3). This may explain why these taxa disappeared from New Zealand during climate cooling. Adaptations to climate cooling involve multiple physiological processes and in thermophilic species may limit growth and disrupt species interactions. For example, many cold-intolerant plant species went extinct in response to early Pleistocene cooling in Japan and Tasmania (Huang et al., 2018; Jordan, 1997). Climate cooling at the Eocene-Oligocene boundary in North America is associated with a complete turn-over in plant composition (Retallack et al., 2004). Climate cooling also induced changes in species interactions at the Cretaceous-Paleogene boundary and was shown to increase seed size in trees in response to more prevalent animal seed dispersal (Cui et al., 2019).

The role of climate cooling in genera extinction in New Zealand is supported by results of one pair in this project. *Ludwigia* went extinct from New Zealand in the middle Eocene when climate cooled after the temperature peaked at the Paleocene-Eocene Thermal Maximum (Hollis et al., 2009; Burgess et al., 2008). Today, *Ludwigia* occupies areas that are warmer with more distinct wet and dry seasons than its New Zealand extant counterpart. These climate shifts from tropical to more temperate conditions may have played a role in its extinction. This is consistent with *Ludwigia*, a genus containing mainly aquatic plants requiring high levels of moisture. Recently, *Ludwigia* has become invasive in many areas, responding to increased temperatures associated with climate change (Gillard et al., 2017b; Gillard et al., 2017a). Gillard et al. (2017b) also found that low precipitation seasonality had a negative relationship with the presence of *Ludwigia* which is consistent with our findings.

Additionally, high summer and wet season temperatures are important for both *Sloanea* and *Ludwigia* (Figure 4.16). This suggests that changes in temperature dynamics may

have a larger impact on *Sloanea* and *Ludwigia's* ability to survive than average temperatures alone. For example, Cunningham and Read (2003) found that the rate of photosynthesis in *Sloanea woollsii* decreased as temperature fell below 24^{O}C, indicating a preference for warm wet seasons.

Sloanea went extinct in New Zealand in the early Miocene, a time of slight climate warming (Prebble et al., 2017; Cooper and Cooper, 1995). This is inconsistent with the climate pattern suggested by the difference in climate niche because *Sloanea* occupies areas that are warmer than its extant counterpart, indicating that *Sloanea* should do well during a period of climate warming. However, some suggest that New Zealand experienced a brief period of climate cooling during the earliest Miocene (Devereux, 1968), which may explain our results for this genus. It is uncertain exactly what temperature changes were occurring during the early Miocene. A direct link between the climate niche of *Sloanea* and its extinction is further questioned by the similarity of the climate niches of *Sloanea* and its other New Zealand extant counterpart *Elaeocarpus* (see Section 5.2.3). The similarity of these two niches suggests that climate was not a factor in the extinction event. It is possible that other factors occurring during that time, such as increased natural migration of Australian plant species, may have had a larger impact on *Sloanea* than climate (see Section 5.2.3; McGlone et al., 2001).

Wetter Niches

Three New Zealand extinct genera, *Mallotus, Cupaniopsis, and Mischocarpus,* occupy areas in Australia today that are distinctly wetter than their New Zealand extant counterparts, suggesting that the loss of consistently wet areas in New Zealand, as a result of climate drying, may have played a role in their extinction. Although temperature variables showed less difference than precipitation variables, those variables with the most difference were seasonality and temperature annual range which suggests that tropical climates with prominent summer precipitation are an important climatic factor for *Mallotus, Cupaniopsis, and Mischocarpus* (Figure 4.16).

Precipitation changes can also have a strong impact on species' ranges. In California, plant species have shifted downslope, in the opposite direction to what is expected under

climate warming (an uphill shift to follow analogous climate), tracking changes in precipitation (Crimmins et al., 2011). This indicates that some species are more responsive to changes in precipitation than temperature. Plants may also take many generations to respond to temperature shifts, based on evidence of the lag in niche tracking during climate warming in the last 16,000 years in North America (Ordonez, 2013). This suggests that species were not able to track changes in either precipitation or temperature as quickly as these climate changes occurred, especially if the emerging climates were novel (Ordonez, 2013).

Mallotus went extinct in New Zealand during the middle Miocene following an abrupt period of climate cooling, compared with the early Miocene (Cooper and Cooper, 1995; Pole, 2014; Prebble et al., 2017). The middle Miocene is associated with a decrease in temperature of approximately 3^{O}C as well as a sharp decrease in precipitation (Pole, 2014). These conditions caused a shift to drier vegetation in the middle Miocene in New Zealand which is consistent with the extinction of the tropical *Mallotus* (Pole, 2014). The middle Miocene was also associated with an increased fire frequency in New Zealand (Pole, 2014). Changes in disturbance patterns can have large effects on community structure and extinction (Cahill et al., 2013). However, some modern species of *Mallotus* (*M. japonicus* and *M. paniculantus*) have shown fast recovery after fire events suggesting that this increase in fire frequency may not have been the mechanism of extinction for *Mallotus* (Goto et al., 1996; Hiratsuka et al., 2006).

Both *Cupaniopsis* and *Mischocarpus* went extinct at the Oligocene-Miocene boundary, approximately 24 MYA, which is associated with the end of a period of climate cooling that occurred throughout the Oligocene (Prebble et al., 2017; Cooper and Cooper, 1995). The results suggest that it was not overall cooling but perhaps changes in temperature seasonality and precipitation that caused the extinction events of *Cupaniopsis* and *Mischocarpus* due to the distinct difference in precipitation preference between *Cupaniopsis* and *Mischocarpus* and their New Zealand extant relative *Alectryon* (Figure 4.16). This is inconsistent with Prebble et al. (2017) who found no change in temperature seasonality or precipitation over the late Oligocene. Additionally, smaller leaf size, an adaption to cooler temperatures, is not different between *Cupaniopsis, Mischocarpus,*

and *Alectryon* suggesting that leaf size of these genera did not change as a response to climate cooling during the late Cenozoic (Reichgelt et al., 2017). Precipitation dynamics are thought to have caused the extinction of other New Zealand angiosperm species in the late Miocene (Lee et al., 2001). This is consistent with our finding that it was changes in precipitation and temperature dynamics and not overall temperature decrease that likely led to the extinction of *Cupaniopsis* and *Mischocarpus*.

Cooler and Drier Niches

Two extinct genera, *Araucaria* and *Acacia*, have drier and cooler niches than their New Zealand extant counterparts, *Agathis* and *Sophora*, suggesting their extinction may have occurred due to climate warming or wetting (Figure 4.12). Both *Araucaria* and *Acacia* occupy areas in Australia that have higher temperature seasonality but lower overall temperatures than their New Zealand extant counterparts and is more pronounced in *Acacia* (Figure 4.16). Additionally, both *Araucaria* and *Acacia* occupy areas that have less warm and wet season precipitation than their extant counterpart but similar cold and dry season precipitation (Figure 4.16).

Araucaria occupies areas in Australia that are cooler and with more consistent precipitation than its New Zealand extant counterpart *Agathis* but is in climates with similar overall precipitation and temperature seasonality (Figure 4.13). Therefore, it is likely that warmer dry season temperatures and greater wet season precipitation were an important determinant of the extinction event. This is consistent with climate warming through the middle Miocene when *Araucaria* went extinct (Pole, 2014). In South America, *Araucaria* forests prefer cool areas without a distinct dry season which has impacted the distribution of *Araucaria* throughout the Quaternary (Behling, 1997; Iriarte and Behling, 2007). *Araucaria* forests in South America have also decreased their range since the LGM in response to warming and are predicted to suffer further range restrictions due to anthropogenic climate change (Bergamin et al., 2019). This is consistent with our results for climate warming and precipitation seasonality being a determining factor in the extinction of *Araucaria* in New Zealand. *Araucaria* is also no longer abundant in Southeast Australia although it was abundant there in the past based on the fossil record (Lee et al., 2016) suggesting that *Araucaria* was able to migrate to

favourable northern climates in Australia but this option was not available in New Zealand.

Acacia went extinct in the middle Pleistocene, 1 MYA, which is inconsistent with the climate areas occupied by *Acacia* today. These areas are cooler than its New Zealand extant counterpart *Sophora*, especially in terms of cold season temperature and temperature seasonality. This is inconsistent with extinction during much of the Pleistocene which was cooler and more seasonal than previous time periods (Prebble et al., 2017; Cooper and Cooper, 1995). This extinction event is also inconsistent with the frost tolerance of *Acacia,* withstanding minimum temperatures as low as -6^{O}C (Searle, 1997). Extinction of *Acacia* occurred during the cool Pleistocene suggesting that temperature change did not lead to extinction.

Acacia covers a large portion of dry areas in Australia with mean annual precipitation and wet season precipitation less than its New Zealand extant counterpart (Figure 4.4, Figure 4.12, and Figure 4.16). *Acacia's* extinction in the middle Pleistocene is associated with an increase in maximum precipitation from approximately 3000 mm/year to up to5000mm/year (Prebble et al., 2017). Minimum precipitation also increased over this period but to a lesser extent than maximum, resulting in an increase in the average yearly rainfall in New Zealand during the Pleistocene (Prebble et al., 2017). This is consistent with the extinction of *Acacia* which occupies areas that are substantially drier than its extant counterpart *Sophora*. *Acacia* fecundity has been shown to decrease as precipitation increases with up to 55% fewer seeds entering dormancy under wetter conditions (Tozer and Ooi, 2014).

Acacia also has substantially more species and a larger climate niche than *Sophora* (Figure 4.9). However, this should not impact extinction risk because niche volume and extinction were not linked in this or other studies (Di Febbraro et al., 2017; Saupe et al., 2015).

Cooler and Wetter Niches

The New Zealand extinct genus *Microcachrys* has a cooler and wetter niche than its extant counterpart *Podocarpus* suggesting that it went extinct during a time of climate

warming and decreased precipitation. However, *Microcachrys* went extinct in the Pleistocene (1 MYA) when New Zealand was becoming both cooler and wetter (Prebble et al., 2017). Due to this inconsistency between changes in climate and the niche of the New Zealand extinct *Microcachrys* there are likely other factors beyond the direct effects of climate change that pushed this genus to extinction in New Zealand.

Microcachrys has a relatively small climate niche, occupying a small range of climates (Figure 4.4 and Figure 4.9). *Microcachrys* is a low-growing alpine shrub requiring open high-altitude habitats outside of forests (Carpenter et al., 2011). A restricted climate niche and limited habitat range may have led to its New Zealand extinction. One theory for the disappearance of *Microcachrys,* despite apparent climatic suitability in New Zealand, is the difference in the intensity of glaciation between New Zealand and Tasmania during the Pleistocene (Carpenter et al., 2011). The Southern Alps experienced heavy glaciation during the Pleistocene while Tasmania only experienced mild glaciation (Colhoun and Barrows, 2011; Colhoun, 2004; Mathews, 1967; Suggate, 1990). Much of the habitat suitable for *Microcachrys* during the Pleistocene may have been heavily glaciated in New Zealand but available in Tasmania (Carpenter et al., 2011). Both *Microcachrys* and *Podocarpus* produce fleshy arils dispersed by birds (Simpson, 2010) and therefore changes in interactions with seed dispersers are unlikely to have been a cause of extinction.

5.2.3 Extinction Events Without Climate Indicators

The climate niches of four New Zealand extinct genera show no distinct climate difference when compared their extant counterparts (Table 4.2 and Figure 4.12). The three genera with similar climate niches and high niche overlap, between their extinct and extant genera are *Sloanea, Cryptocarya,* and *Caesalpinia.* The fourth New Zealand extinct genera, *Agrophyllum*, has a statistically similar climate niche to its extant counterpart but has low niche overlap due to differing niche volumes, with the extant genus' climate niche completely contained within the extinct genus's climate niche (Figure 4.12).

High Climate Niche Overlap

Three New Zealand extinct genera showed no difference in their climate niches with their New Zealand extant counterpart with both extinct and extant genera occupying similar niche dimensions. These genera are *Sloanea* (one pair), *Cryptocarya* (two pairs), and *Caesalpinia* (one pair). Both *Cryptocarya* and *Caesalpinia* extend to the warmest and wettest portions of the Australian climate space (Figure 4.12). When *Cryptocarya* is compared to both the New Zealand extant counterparts, niches were similar. In contrast, *Caesalpinia* was determined to be significantly different from its New Zealand extant counterpart (*Sophora*) with a niche that extends into drier areas than *Sophora* (Table 4.2 and Figure 4.12). However, both *Cryptocarya* and *Caesalpinia* have high climate niche overlap with their New Zealand extant counterparts meaning that the extant genera cover much of the same climate area as those that are extinct (Table 4.2). There is no clear indication that climate was a factor in the New Zealand extinction of either *Cryptocarya* or *Caesalpinia*.

For *Caesalpinia*, this may be explained by land area availability. The New Zealand extinction age of *Caesalpinia* coincides with the period of maximum marine transgression in New Zealand (28 MYA). *Caesalpinia* is the only genus in this study with an extinction age during this period, and no other angiosperm genera are known to have gone extinct at this time (Lee et al., 2001). During this period, New Zealand was broken into a series of low-lying islands with land area reduced by up to 80% from present day (Cooper and Cooper, 1995). Habitat loss is one of the primary known causes of extinction (Krauss et al., 2010; Guardiola et al., 2013). Extinction from habitat loss due to sea-level rise was seen during the Pleistocene in Bermuda which underwent a large reduction in land area followed by the extinction of many bird species (Olson and Wingate, 2000). In addition to reduced land area, smaller islands have more exposure to storms which has been shown to cause high levels of local plant extinction (Burns and Neufeld, 2009).

Extinction rates are known to be higher on islands (Rosenzweig, 1995),therefore the splitting of New Zealand into small islands during the Oligocene is consistent with increased extinction. Smaller areas have fewer species reflecting limited habitats (Rosenzweig, 1995) and has been used to predict extinction risk based on habitat loss (He

and Hubbell, 2011). However, the importance of these factors likely overestimates species loss due to a reduction of habitat because of the difficulty in discerning the difference between colonizing new area and persisting in a location, albeit a smaller area, that was already colonized (He and Hubbell, 2011). This overprediction of extinction due to habitat loss may be reflected in the limited extinction of genera during the Oligocene in New Zealand (Lee et al., 2001).

Both *Cryptocarya* and *Sloanea* became extinct after maximum marine transgression during a time of climate warming in the early Miocene (20 MYA; Cooper and Cooper, 1995; Prebble et al., 2017). Climate warming may have had an impact on *Cryptocarya* and *Sloanea's* ability to survive through changes in species interactions or disturbance regimes that are not reflected in the current realized niche of these genera (Cahill et al., 2013). For example, insect pollination is the prevalent reproductive method in both genera families, Lauraceae and Elaeocarpaceae (Sampson and Berry, 2019; Matthews and Endress, 2002), and therefore changes in pollinator abundance during this time may have impacted *Cryptocarya* and *Sloanea's* ability to survive. Shifts in timing of flowering and pollination, attributed to climate changes, may have the potential to be extreme and sufficient enough to cause extinction of plants and their pollinators (Memmott et al., 2007).

During the early Miocene New Zealand had low-lying newly formed areas and subtropical climates similar to Australia. The availability of relatively vacant niches resulted in a high level of long-distance dispersal and colonization from Australia, including *Eucalyptus* which appeared in New Zealand during the Miocene (McGlone et al., 2001; Lee et al., 2016). These colonization events may have introduced competitors for *Cryptocarya* and *Sloanea*, leading to their extinction. Competition mediated extinction has been seen in many ecosystems over different time periods and the introduction of a new species can alter the community structure to such an extent that native species can no longer persist (Mack et al., 2000; Cahill et al., 2013; Lewin, 1983). For example, the decline of an endangered coastal dune plant was exacerbated by the introduction of an invasive grass which outcompeted and increased herbivory of the native plant (Dangremond et al., 2010). Competition may also increase the likelihood of

an extinction cascade, i.e. the extinction of a plant may lead to the extinction of the pollinator (Bewick et al., 2013). Therefore, both changes in plant-pollinator interactions and new competitors may have been severe enough to lead to the extinction of *Cryptocarya* and *Sloanea*.

Although the New Zealand extinct genus *Sloanea* shows no difference in niche with the New Zealand extant genus *Elaeocarpus*, it does show a difference in niche with its other New Zealand extant genus *Aristotelia*. The role of climate in *Sloanea's* extinction is less clear than for *Cryptocarya* and *Caesalpinia*. It is important to note that *Elaeocarpus* has substantially more species and a larger niche volume, 26 species and 0.31 Schoener's D respectively, than *Sloanea*, 4 species and 0.22 Schoener's D respectively (Figure 4.12). Although climate niche volume alone is unlikely to determine extinction risk (Di Febbraro et al., 2017; Saupe et al., 2015). The comparison of *Sloanea* with its other New Zealand extant genus, *Aristotelia,* did not match the climate conditions during the time of extinction (see Section 5.2.2). The combination of these two results, one pair being statistically similar and one pair not matching changes in climate conditions, indicates that direct climate dynamics are unlikely to be the cause of the extinction of *Sloanea*.

Low Climate Niche Overlap

The climate niche of the New Zealand extinct *Argophyllum* completely contains the climate niche of the New Zealand extant *Corokia.* These two niches are climatically similar, especially for precipitation, temperature, and seasonality (Table 4.2, Figure 4.12, and Figure 4.16). These two genera do not have niches of the same size, with *Argophyllum* having a much larger niche volume than *Corokia* (Figure 4.9 and Figure 4.12). *Argophyllum* became extinct in New Zealand during a period of climate warming in the early/middle Miocene (18 MYA; Prebble et al., 2017; Cooper and Cooper, 1995; Pole, 2014). There is no indication in the climate niche of *Argophyllum* suggesting that climate was the mechanism causing the extinction. In fact, *Argophyllum* occurs in areas today that are climatically similar to those of the early/middle Miocene (Figure 4.2 and Figure 4.4). As discussed previously, warming climates have had impacts on pollinators and herbivores that may have led to the extinction of *Argophyllum* (Cahill et al., 2013).

However, little is known about *Argophyllum's* interactions with pollinators, dispersers, and herbivores and therefore the mechanism of this extinction is difficult to ascertain.

5.3 CLIMATE NICHE SHIFTS

New Zealand split from Australia approximately 80 MYA with subsequent speciation and colonization of taxa occurring after separation (Sanmartin and Ronquist, 2004; McGlone et al., 2001). The aim of this investigation is to determine the amount of niche conservation or divergence that has occurred between the Australian and New Zealand distributions of extant New Zealand plant genera since the time of separation or colonization to understand how these extant genera survived climate cooling in New Zealand. This study investigated the differences in climate niche between the Australian and New Zealand distributions of the same genus and are described in this section, specifically looking to determine the degree of niche shift within genera.

5.3.1 Niche Difference Between Australian and New Zealand Distributions

Throughout the Cenozoic the climate of New Zealand has cooled compared to Australia, specifically differentiating itself in the Pliocene and Pleistocene as New Zealand underwent extreme climate cooling and mountain building (Prebble et al., 2017; Lee et al., 2001). The New Zealand distributions of most extant focal genera are found in environments that are cooler with more consistent year-round rainfall than in Australia. *Aristotelia*, *Epilobium*, and *Podocarpus* occupy areas that are more similar to their Australian counterpart than other genera, specifically in terms of temperature and precipitation seasonality (Figure 4.22). All genera except, *Agathis, Beilschmiedia,* and *Alectryon,* overlap more in terms of temperature and precipitation seasonality than is witnessed between the climate space of Australia and New Zealand. This pattern suggests these genera, in New Zealand and Australia, are more concentrated in the common climate space than would be expected based on comparison with the climate space available in both countries. This concentration of New Zealand distributions in the warmest part of the New Zealand climate space, i.e. those areas that are most similar to Australia in terms of temperature and precipitation seasonality, is consistent with late

Cenozoic climate cooling (Prebble et al., 2017) since those genera that survived in New Zealand would occupy warmer areas consistent with past New Zealand climate analogues in Australia.

The fact that New Zealand extant genera occupy cooler areas than their Australian relatives generally is consistent with New Zealand species adapting to cooler climate through the late Cenozoic. Reichgelt et al. (2017) found that the average leaf size of angiosperm species in New Zealand has decreased in response to cooling through the Pliocene and Pleistocene, reflecting trends globally (Wright et al., 2017). Leaf sizes of modern plants in New Zealand are smaller when compared to species within the same family in Australia and New Caledonia (Reichgelt et al., 2017). Specifically, *Beilschmiedia*, which has low overlap with its Australian distribution in terms of temperature, also has smaller leaf sizes in New Zealand than in Australia (Reichgelt et al., 2017).

For most extant genera, the New Zealand distributions occupy areas that experience both cooler winter minimum and cooler summer maximum temperatures (Figure 4.25) suggesting that neither parameter had significantly more impact on niche shift. This is inconsistent with Araujo et al. (2013) who found that cold tolerance limits varied significantly more than heat tolerance limits, suggesting that upper heat tolerance has remained stable over large taxonomic groups while cold tolerance is more likely to shift. Two genera, *Euphoria* and *Alectryon*, show a greater shift to cooler warm season temperatures in New Zealand with little difference in winter temperatures between distributions (Figure 4.25). This suggests that it was warm season temperatures and not cold season temperatures that contributed more to niche shift in these two genera.

There is no difference in niche volume between the Australian and New Zealand distributions of the New Zealand extant genera (Figure 4.20). Niche volume and geographic range of genera are linked, in that species with larger geographic ranges have expanded niche volumes (Granot and Belmaker, 2019; Vazquez and Stevens, 2004). However, some New Zealand extant genera have a climate niche that is larger in Australia than New Zealand likely due to the larger geographic space available in

Australia. This can be seen in the genera *Euphorbia* and *Alectryon* which have larger Australian geographic distributions and climate niche volumes (Figure 4.4 and Figure 4.18). However, niche volume has been shown not to affect the rate of niche evolution, with large and small niches changing at a similar rate (Fisher-Reid et al., 2012). This suggests that differences in niche volume are not contributing to the overall trends of niche conservation and divergence in the focal genera.

5.3.2 Niche Divergence or Conservation

Niche divergence has been quantified in several ways (Guisan et al., 2014). The two most common tests are Schoener's D and the niche similarity test (Warren et al., 2008; Cardoza-Martinez et al., 2019; Dreyer et al., 2019; Filz and Schmitt, 2015; Iosif et al., 2014; Petitpierre et al., 2012). Most studies use both metrics and have found that when niches are significantly similar, Schoener's D is also moderate to high. For example, Warren et al. (2008) showed that most niches of closely related butterfly, bird, and mammal species had statistically similar niches between sister taxa. However, Warren et al. (2008) were investigating sister species within the same environment and most pairs had moderate Schoener's D values. These metrics have also been used to compare the current and future predicted ranges of species. Hamid et al. (2019), investigating *Betula utilis*, found that niches will likely be conserved under future climate change, based on high Schoener's D values as well as statistical similarity.

This study found that all pairs of New Zealand extant genera have very low climate niche overlap between their New Zealand and Australian distributions which is consistent with low overlap between the two countries (Table 4.4 and Figure 4.21). However, the degree to which niches have diverged is context dependant and should take into account changes in climate between the two regions that occurred through the Cenozoic. When considering the difference in available climate space between the two continents eight of the eleven genera (72 percent) were more similar to each other than expected by chance meaning these genera likely conserved their niches through time (Table 4.4). Dreyer et al. (2019) found that between *Ligustrum lucidum's* native range, temperate Asia, and one of its invaded ranges, North American west coast, niches did not diverge

despite low niche overlap (Schoener's D of 0.09). This is consistent with our findings that, despite low overlap, niches may be conserved.

Niche conservation has been seen for numerous plant species over different time periods. For example, many tree species have stable climate niches through the Quaternary, repeatedly undergoing migrations to track suitable climate instead of adapting locally to new conditions in Europe (Pearman et al., 2008b; Rodríguez-Sánchez and Arroyo, 2008) and North America (Martínez-Meyer and Peterson, 2006). This niche conservation is consistent with eight of the genera in this study (*Agathis*, *Corokia*, *Aristotelia*, *Euphorbia*, *Sophora*, *Beilschmiedia*, *Epilobium*, and *Alectryon*) based on the results from the niche similarity test (Table 4.4).

Disparity between low overlap and statistical niche significance is seen for many genera. For example, Australian and New Zealand distributions of *Beilschmedia* and *Litsea* have climate niche overlaps of 0.02 with similar niche characteristics and distributions along the PCA axes (Table 4.4, Figure 4.21, and Figure 4.22). However, according to the niche similarity metric, when the difference in available climate space is accounted for, the niches of *Litsea* are not similar, whereas the niches of *Beilschmedia* are similar. This is likely because the maximum occurrence density of *Litsea* is further outside the common climate space than *Beilschmedia* (Figure 4.22). These disparities are likely a reflection of the large difference in available climate between Australia and New Zealand which is known to cause problems in determining niche change dynamics (Guisan et al., 2014). Dreyer et al. (2019) did not disclose the climatic areas used in determining niche similarity and therefore the environmental background conditions in their study may have been more similar than in this study which would explain the differences in our results. Overall, our results indicate that the niches of eight genera are similar and three genera are different between their Australia and New Zealand distributions. However, due to the low overlap between the climate availability, other factors should be examined to determine the level of niche shift occurring (Guisan et al., 2014).

The genera that have conserved their climate niches between their New Zealand and Australian distributions still show large differences in occupied climate between

Australia and New Zealand. This may indicate a shift in the realized climate niche of these genera. Pearman et al. (2008b) found that *Juniperus communis* underwent niche shift in Europe in response to glacial cycles likely due to habitat and competition dynamics rather than climate. This plasticity in plants has been shown in many species where populations are differentially adapted to the climates in which they live (Davis and Shaw, 2001). For example, northern populations of Scots pine (*Pinus sylvestris*) in Sweden are better adapted to cold and have lower mortality in cold climates than southern relatives (Davis and Shaw, 2001). Due to this high level of plasticity in plants, the differences in realized niche between Australian and New Zealand distributions may be due to habitat availability, dispersal ability, and species competition instead of climate availability.

Three genera in this study were determined to have different climate niches in New Zealand and Australia and have likely undergone niche divergence. These genera are *Elaeocarpus*, *Litsea*, and *Podocarpus* (Table 4.4). Niche divergence can occur over geologic time in response to adaptation to specific environments. This is consistent with niche shifts of New Zealand tree fern species when compared to their global relatives (Bystriakova et al., 2011). Specifically, Bystriakova et al. (2011) found that New Zealand tree ferns preferred climates that were significantly cooler than other closely related taxa. This is seen in both *Elaeocarpus* and *Podocarpus* which occupy cooler areas that extend far outside the New Zealand-Australia common climate area (Figure 4.21). Furthermore, *Podocarpus*, occupies a large amount of the common climate space with the New Zealand and Australian distributions occupying many of the same areas in common climate space. This niche stability in common climate space is opposite to what would be expected for niche divergence. Therefore, it is important to understand how the dynamics of the niche in common climate space and total climate space interact to fully understand niche changes (Guisan et al., 2014).

Although climate niches have been conserved for most of our study genera, differences in available climate have forced New Zealand plants to occupy areas cooler than their Australian counterparts. This may be a shift in the realized niche between the two

distributions but for eight of the eleven genera this shift was not large enough to constitute niche divergence.

5.3.3 Niche Differences in Common Climate

Eight genera have conserved climate niches and therefore it is expected that both distributions (New Zealand and Australia) will have high overlap climate space that is common between Australia and New Zealand. This is because common climate space is geographically available to all genera in both countries. However, of the eight genera that are significantly similar between distributions, approximately half (9 out of 16 distributions) only occupy a small (less than 50 percent) portion of the common climate (Figure 4.23). This is similar to *Quercus rubra* whose invasive and native niches were statistically similar but with a large amount of unoccupied common climate area in its invasive range (Camenen et al., 2016).

A large amount of unoccupied common climate space may be the result of less contiguous common climate areas in Australia than in New Zealand which may decrease the habitat availability, limit dispersal, and increase the likelihood of competition or predation in Australia (Figure 4.3). These species may be excluded from areas of common climate in Australia for reasons other than climate, such as competition for space or an inability to disperse into areas of common climate (Table 4.3). For example, dispersal ability has been linked to an increased likelihood of niche changes due to plants being able to occupy and adapt to new areas (Aguilee et al., 2016). If genera are not able to move into common climate in Australia, due to lack of dispersal or competitive restriction, then their realized niches will not reflect their fundamental niche. Hutchinson (1957) considered competition as the main factor in constraining the fundamental niche. Therefore, interspecific competition in Australia that does not occur in New Zealand may be contributing to the low levels of niche overlap with common climate space in Australia.

New Zealand genera have undergone a high level of niche expansion (Table 4.5) based on the New Zealand distributions occupying a larger portion of the common climate area than their Australian counterparts. This is considered niche expansion because the climatic conditions currently seen in New Zealand have only existed since the

Pleistocene. New Zealand therefore has higher climate novelty compared to Australia which still contains climates similar to those experienced during most periods of the Cenozoic (See Section 5.1). Niche expansion of the New Zealand extant genera distributions in common climate space may be caused by increases in habitat availability and release from competition or predation (Guisan et al., 2014) associated with climatic changes in New Zealand in the late Cenozoic.

All New Zealand genera distributions, except *Podocarpus* (discussed below), occupy a greater portion of the common climate space than their Australian distributions (Figure 4.23). Specifically, New Zealand distributions occupy areas that are cooler with more consistent rainfall and do not occupy areas with low total annual precipitation and highly seasonal temperature. However, some New Zealand distributions do occupy areas that are drier in common climate space (e.g. *Sophora*) while others occur in wetter areas (i.e. *Epilobium*) but most genera occupy areas that are similar in precipitation and temperature seasonality in common climate space (Figure 4.22). New Zealand niche expansion into cooler areas is consistent with climate cooling during the late Cenozoic (Prebble et al., 2017).

One possible explanation for niche expansion in New Zealand is the release from competition or predation that may be occurring in Australia but not in New Zealand. Competition and predation are known to control distributions of many species. For example, Bolnick et al. (2010) found that after removal of top predators, stickleback fish expanded their niche. In plants, herbivory can have large impacts on range limits and has shown to effectively restrict species dispersal into new areas (Speed et al., 2010; Hillyer and Silman, 2010). This may be particularly important since New Zealand does not have the native terrestrial mammals that are common in Australia. Competition for light in saplings also constrains range limits of trees (HilleRisLambers et al., 2017) and competition negatively impacts seed production of adult plants resulting in a similar limits to species ranges (Stanton-Geddes et al., 2012). Release from competition induced restraints may have contributed to the niche expansion of the New Zealand distribution of extant genera.

Niche expansion in new areas may have occurred due to the creation of new mutualisms in the invaded range (Mitchell et al., 2006). It has been shown that gain or loss of a mutualism can either expand or limit a species range (Chalcoff et al., 2012; Moeller et al., 2012; Young et al., 2012). These mutualisms can directly cause niche changes. Afkhami et al. (2014) showed that mutualisms between soil fungi and grasses allow for grasses to occupy areas that are drier and more stressful, thereby shifting the species realized niche. Therefore, differences in species interactions between New Zealand and Australia may explain the difference in the amount of occupied common climate.

In addition to climate cooling, mountain building occurred in New Zealand in the late Cenozoic, creating new habitats which may have facilitated niche expansion of the New Zealand distribution. These new habitats are a combination of both biotic and abiotic features that affect species survival beyond climate and species interactions alone (Mitchell, 2005). Habitat includes features on the landscape such as elevation, soil quality, or proximity to water, that affect a species distribution (Kearney, 2006). For example, Australian habitats are marked by nutrient poor soils (Orians and Milewski, 2007). When directly compared to New Zealand, Tasmanian soils are more phosphorus limited than New Zealand soils (Wright et al., 2010) which may constrain plants' ability to survive in Australia but thrive in New Zealand despite having similar climates.

Disturbance type and frequency may also contribute to the difference in niches between Australian and New Zealand distributions, specifically the niche expansion of the New Zealand distribution in common climate space. Fire is an important factor in Australian ecosystems perhaps since the beginning of the Cenozoic (Crisp et al., 2011; Orians and Milewski, 2007). For example, fire tolerant trees species, such as those in the family Myrtaceae (including *Eucalyptus*), dominate Australian forests (Crisp et al., 2011). Fire frequency and severity is low in New Zealand forests with many New Zealand species having sensitivity to fire, especially early successional species (Kitzberger et al., 2016).

In contrast to those genera which show large differences in common climate space, *Podocarpus* shows a high level of niche stability within the common climate space but has also extended its niche far outside the common climate area. This suggests that

instead of being released from competition or predation, *Podocarpus* has evolved to occupy newly established cool mountainous areas throughout New Zealand, including one species found in alpine areas of the Southern Alps. For example, when comparing the Australian and New Zealand alpine species of *Podocarpus* (*P. lawrencei* and *P. nivalis* respectively), the New Zealand species occupies areas that are on average cooler and wetter than the Australian species (Biffin et al., 2012).

The methodology for determining when a niche should be considered conserved or diverged is still inconsistent (Guisan et al., 2014). However, there is evidence that most niches have been conserved between Australia and New Zealand and release from competition, or increased habitat availability may explain why New Zealand distributions occupy a larger portion of the common climate space than Australian distributions.

5.4 Methodological Limitations and Future Directions

Niche models have inherent assumptions and biases. They assume that the current distribution of a species is in equilibrium with climate and is a reflection of the realized climate niche (Guisan and Thuiller, 2005; Pearson and Dawson, 2003). Inherently, this climate niche does not include other factors which may contribute to the distribution of a species. These include species interactions and lags in dispersal (Guisan and Thuiller, 2005; Pearson and Dawson, 2003). Additional studies to understand how factors other than climate may be affecting the realized niche of each group would improve understanding.

Large differences were seen in Schoener's D and the similarity metric when including and excluding available climate as a variable in the calculation if the available climate differs greatly. The determination of niche conservation or divergence when two distributions have large differences in available climate has not been explored in the literature. Other studies have explored the best methods for quantifying niche overlap (Broennimann et al., 2012). Similar tests that provide consistency in determining when there is niche conservation or divergence, regardless of the difference in available climate, would help provide further clarity for this project.

The dates of extinction are based on the last known fossil record and new discoveries could indicate more recent extinction dates. New Zealand past climate estimates are also still being explored to clarify the magnitude and timing of climate change at certain time periods, especially with regards to precipitation estimates (Pole, 2014; Prebble et al., 2017). Future studies which provide more precision about New Zealand Cenozoic climate estimates would improve this study.

This project explored climatic differences between extinct and extant genera and provides insight into how climate may have caused these extinctions in the past in New Zealand. However, the abiotic and biotic responses to these changes in climate could be further explored in future studies. Proximate causes of extinction, as defined by Cahill et al. (2013), are mechanisms that are caused by climate changes, such as disrupted species interactions or increased disturbance, but are not directly related to changing climates, i.e. physiological tolerances. Additional information on how these proximate causes induce extinction in plant species would help to provide better context for this study.

This project also investigated the level of niche difference between distributions of the same genera which provided insight into how species may have adapted to new and differing climates. Future studies could enhance this work through understanding the genetic differences within taxa to see if genetic divergence and niche divergence are connected at a species level. Genetic analysis has gained popularity and is increasingly used to understand biogeographic patterns over space and time (Crisp and Cook, 2013; Willis and McElwain, 2014). Additional information on the genetic divergence and species level niche models would provide further insights into the dynamics of niche evolution.

Chapter Six

6 CONCLUSION

Climate is a key driver of plant evolution and extinction, with changes in climate contributing to global species extinctions in the geologic past (Hoffmann and Sgro, 2011; Parmesan, 2006; Wing, 2004; McElwain and Punyasena, 2007). Recent climate change has already contributed to population and range changes with future climate changes expected to further increase the risk of extinction (Cahill et al., 2013; Urban, 2015). The New Zealand flora is highly vulnerable to future climate related extinctions because of local endemism, fragmented distributions, and geographic isolation in the Southern Hemisphere (Urban, 2015). To better understand the vulnerability of New Zealand's plants to future climate change, it is important to understand how New Zealand plants responded to climate changes in the past. This investigation provided insight into these past changes by comparing the climate niches of New Zealand extinct and extant plant genera which currently occur in Australia.

During the Cenozoic many New Zealand plant taxa went extinct (Lee et al., 2001; Lee et al., 2016). Prior to this study it was assumed that climate cooling caused most of these extinctions with little speculation about the role of precipitation and seasonality. Climate cooling of terrestrial environments occurred throughout most of the Cenozoic with one period of warming in the early Miocene when the climate was sub-tropical. During the Pleistocene, extreme temperature fluctuations occurred, with warm-temperate climates during interglacial periods. The study established that all New Zealand Cenozoic climates are currently found in Australia due to Australia's broad latitudinal coverage allowing for

the use of Australian climate to understand New Zealand climate dynamics during the Cenozoic. This showed that most New Zealand extinct taxa occupy significantly different climates than their New Zealand extant relative. The climate features that most differentiate extant and extinct genera are total precipitation and both precipitation and temperature seasonality.

Not all differences in climate niches between the extinct and extant genera in this study are consistent with climate cooling. Only two pairs have a strong correlation with climate cooling (*Sloanea* vs. *Aristotelia* and *Ludwigia* vs. *Epilobium*). All other pairs with different climate niches have a stronger correlation with differences in precipitation and seasonality than with changes in mean annual temperature. Some extinct genera occupy areas that are less temperature seasonal with more precipitation and others occupy areas that are more temperature seasonal with less precipitation. Based on these study results, it is likely that climate variables such as precipitation and seasonality, either in a movement to more tropical or more temperate climate patterns, were the driving climatic force for many past plant extinctions in New Zealand and mean annual temperature alone was not crucial to these extinction events.

New Zealand and Australia share many plant families and genera with a common history although New Zealand has a current climate that is much cooler than most of the Australian climate. To better understand why some shared plant taxa survived climate cooling in New Zealand, the difference in climate niches between the New Zealand and Australian distributions of taxa currently extant in New Zealand were analysed. The New Zealand distributions of most New Zealand extant genera niches are not significantly different from the niche of their Australian relatives, suggesting that the climate niches of these genera have been conserved through time. The current New Zealand distributions of these genera cover a wider range of cool temperate climates within climate space that is geographically available to both distributions. This suggests New Zealand distributions experienced a release from competition or predation or an increase in available habitat that caused expansion into those climate areas in New Zealand but not in Australia. The New Zealand extant genera investigated here have undergone niche

shift but not complete niche divergence from their Australian relatives, suggesting that niche divergence was not the cause of their survival through the Cenozoic.

Species have already gone extinct as a result of recent anthropogenic climate change which is projected to increase (Humphreys et al., 2019; Bellard et al., 2012). This project has shown that changes in precipitation and seasonality may be a more important climate indicator of extinction risk in plants than temperature alone. Plant taxa also show an ability to shift their climate niches under changing climate which may have contributed to those taxa surviving Cenozoic climate change in New Zealand. This investigation contributes to filling the gap of why plants go extinct by providing a deeper understanding of the dynamics of past plant extinctions in New Zealand.

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